

**RADIATION OF ENDEMIC SPECIES FLOCKS IN ANCIENT LAKES:  
SYSTEMATIC REVISION OF THE FRESHWATER SHRIMP *CARIDINA* H. MILNE  
EDWARDS, 1837 (CRUSTACEA: DECAPODA: ATYIDAE) FROM THE ANCIENT LAKES  
OF SULAWESI, INDONESIA, WITH THE DESCRIPTION OF EIGHT NEW SPECIES**

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**ABSTRACT.** – The ancient lakes of the Indonesian island Sulawesi harbour two endemic species flocks of the freshwater shrimp genus *Caridina* (Crustacea: Decapoda: Atyidae). One of them forms the largest radiation within the genus. Species from both lake systems evolved under similar extrinsic conditions and show some parallel patterns, e.g. the development of unusual and flamboyant colour patterns. After extensive sampling and field observations over several years, we here present the first comprehensive revision of all ancient lakes species from both lake systems. We describe eight new and synonymize one previously described species. Besides standard morphology-based species descriptions of alcohol preserved material, we also provide ecological and behavioural data as well as colour patterns of living animals whenever available. We further use a molecular phylogeny, based on the mitochondrial genes 16S and COI, to support our morphology-based species descriptions. The revision reveals that the total number of species (21) is almost twice as high as previously described. However, there is a considerably lower number of species in Lake Poso than in the Malili lakes, which might be explained by an age difference between the two species flocks or the less pronounced geographical structure of Lake Poso. The molecular phylogeny further suggests the existence of several cryptic species. Last but not least, we hint at conservation priorities, not only for the beautiful shrimps we present in this study, but also for all other organisms endemic to the ancient lakes of Sulawesi that are threatened with extinction by human impact.

**KEY WORDS.** – Sulawesi, Atyidae, *Caridina*, radiation, biodiversity, taxonomy.

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## INTRODUCTION

Ancient lakes, with their often highly diverse and speciose endemic fauna, are natural laboratories for the study of species and speciation. Recently, two ancient lake systems in the central highlands of the Indonesian island Sulawesi (Fig. 1) have been discovered as promising new model systems: both are not only older, larger and deeper than other lakes on the island, e.g. Lake Lindu in Central Sulawesi or Lake Tondano in North Sulawesi, but their biodiversity is also extraordinarily high due to the spectacular radiations of their inhabitants.

The Malili lake system and Lake Poso (Fig. 1B–C) are completely isolated from each other. Age estimates range from more than one million years (Brooks, 1950; Haffner et al., 2001) to a maximum of five million years (Robert Hall, pers. comm. 2007). The solitary Lake Poso is drained by the Poso River towards the north into Tomini Bay (Fig. 1B). The Malili lake system consists of five connected lakes that are drained by the Larona River (Fig. 1C) towards the west into Bone Bay. The northernmost Lake Matano is connected to Lake Mahalona via Petea River and further to Lake Towuti via Tominanga River. The two satellite lakes Lontoa [Wawontoa] and Masapi are not directly connected to the three major lakes. Lake Lontoa is indirectly connected to Tominanga River and Lake Masapi to Larona River. The longitudinal shape of Lake Poso and Lake Matano, the northernmost lake of the Malili system, may resemble typical graben lakes (compare Haffner et al., 2001 for Lake Matano) like Lake Baikal or Lake Tanganyika, but today, they are generally not regarded as such. Lake Poso (323 km<sup>2</sup>) has only one deep basin with a depth of 450 m (Abendanon, 1915; Haffner et al., 2001), whereas Lake Matano and Lake Towuti each have two deeper basins. With a depth of almost 600 m, Lake Matano represents the eight deepest lake in the world (the deepest in Southeast Asia). With 203 m in depth, Lake Towuti is distinctly shallower, but with 560 km<sup>2</sup> more than three times as large as Lake Matano and represents the second largest lake in Indonesia (Giesen, 1994). The depth of the three smaller Malili lakes is approx. 2–4 m (Lakes Lontoa and Masapi) and 73 m (Lake Mahalona). Further, both are ultra-oligotrophic, meaning a high water transparency (approx. 11 m in Lake Poso and more than 20 m in L. Towuti and L. Matano) and an extremely low nutrient and organic content (Giesen et al., 1991; Giesen, 1994; Haffner et al., 2001). This may play an important role in the regulation of species abundance and diversity (Haffner et al., 2006). Temperatures in Lakes Matano, Mahalona, and Towuti vary between 27 and 31°C, a stable thermo- or chemocline is basically missing (isothermal mixing; also constant with depth in Lake Matano: pH 7.4 and conductivity

224 µS). However, the concentration of dissolved oxygen is not maintained with depth (Crowe et al., 2008).

The ancient lakes of Sulawesi are fertile grounds for the adaptive radiation of several and largely endemic species flocks of vertebrates and invertebrates (fishes: e.g. Herder et al., 2006, 2008; snails: e.g. von Rintelen et al., 2004, 2007c; crabs: e.g. Schubart & Ng, 2008; Schubart et al., 2008). This paper reports on two endemic species flocks of atyid freshwater shrimps (Crustacea, Decapoda, Caridina) that represent two of the larger radiations within these lakes. The Malili radiation forms the largest radiation within the genus *Caridina* (von Rintelen et al., in review). The majority of the species have evolved as the result of adaptive radiations, and their ecological adaptations seem to have played a major role in speciation (von Rintelen et al. 2007a, in review). According to these authors, several substrate specialists have evolved in the two lake systems. In contrast, only a few unspecialized species (generalists) today exist. A number of the lacustrine species exhibit unusual and flamboyant colour patterns that are species-specific (Zitzler & Cai, 2006; von Rintelen et al. 2007a; in review), and likewise might have driven intralacustrine diversification (von Rintelen et al., in review). In consequence of the lake radiations, the two species flocks comprise a high number of largely endemic species: 14 are currently described, four from Lake Poso and ten from the Malili lake system (Tables 2–3).

The first to mention atyid shrimps from the two lake systems was Schenkel (1902), who described three species from Lake Poso and its drainage based on a collection by the Swiss naturalists F. and P. Sarasin (Sarasin & Sarasin, 1905). Schenkel's species were later mentioned by Bouvier (1925), Roux (1904), and Woltereck (1937a, b). The majority of the Malili species were described by Woltereck (1937a, b) based on her father's collection from 1932 (Woltereck, 1933a, b). The riverine species *Caridina opaensis* Roux, 1904, originally described from Southeast Sulawesi, was reported as the only non-endemic shrimp from the Malili lakes (Woltereck, 1937a, b). Then, for almost 70 years the state-of-the-art remained unchanged. Brooks (1950) and Chace (1997) mentioned the species from the lakes, but basically referred to Schenkel (1902) and Woltereck (1937a, b). Only in 2006, another new species, *C. spongicola*, was described by Zitzler & Cai from Lake Towuti, the largest of the Malili lakes. Roy et al (2006) published a small-scale study on *C. lanceolata* Woltereck, 1937a from the Malili lakes. Cai & Wowor (2007) revised the Poso species flock and described one new species. Recently, Cai et al. (2009) described two new species from the Malili lake system and redescribed four. Based on morphological and genetic data, von Rintelen et al. (2007a, b) suggested a high number of yet undescribed species in both lake systems, which we here describe. Unfortunately, Woltereck's type specimens could not be traced (KvR & YC, personal observation) and have probably been lost during the Second World War as has some of the fish type material in the most likely depository, the Zoologische Staatssammlung München, Germany, from the ancient lakes (Kottelat 1990a, b). The collections of the museums in Berlin, Frankfurt, Hamburg,

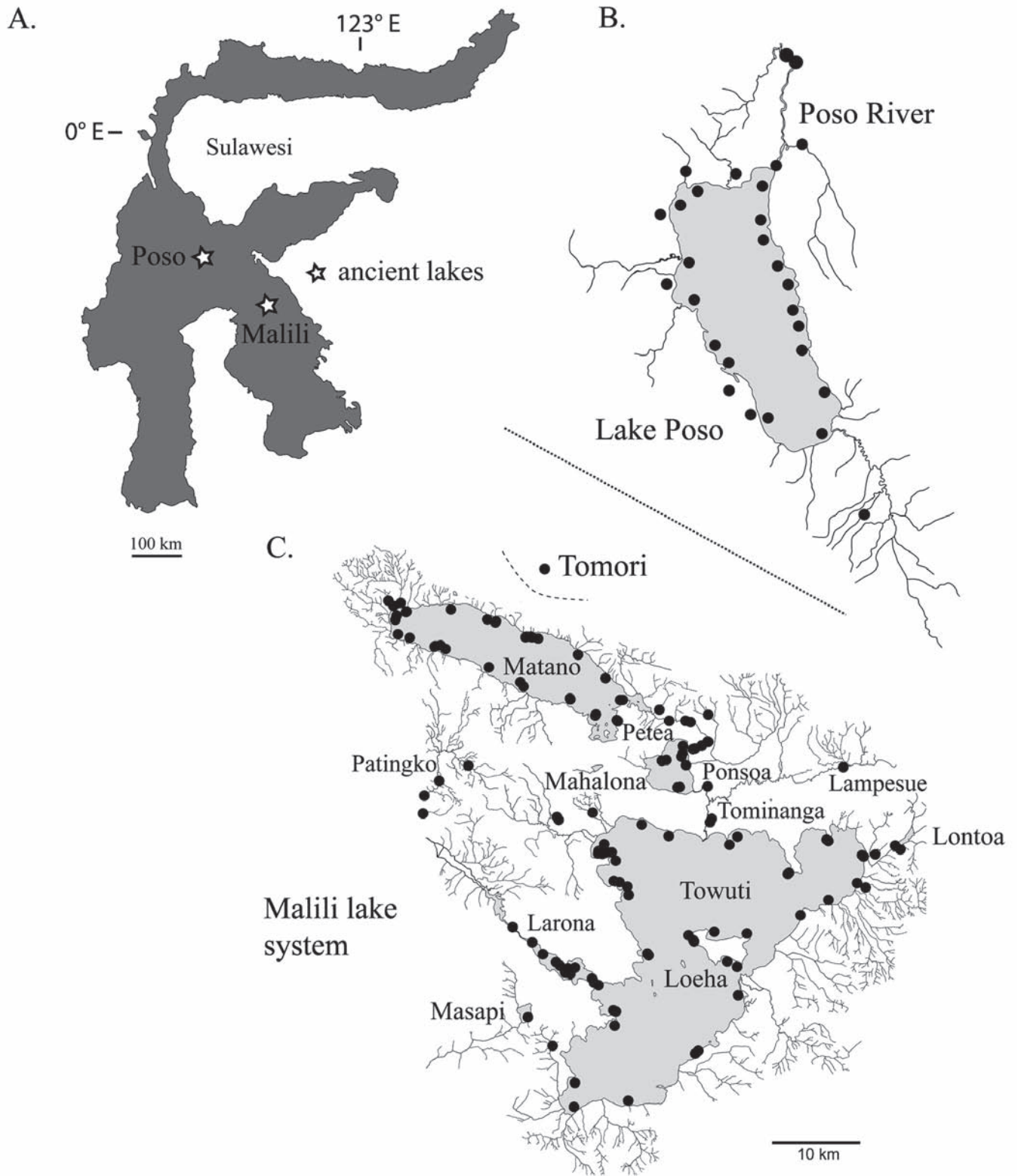


Fig. 1. The ancient lakes of Sulawesi. A. The two ancient lake systems on the Indonesian island Sulawesi. B. Overview of *Caridina* collecting sites from Lake Poso. C. Overview of *Caridina* collecting sites from the Malili lake system.

and Leipzig were checked as well. Cai et al. (2009) also mentioned that Woltereck's types are no longer extant and hence designated neotypes for four species they redescribed. Following this approach, and to complete the redescription of all of Woltereck's species, we here redescribe and designate neotypes for *C. lingkonae* Woltereck, 1937a and *C. tenuirostris* Woltereck, 1937a that have not been examined by Cai et al. (2009).

Here, we revise all species from both ancient lake systems of Sulawesi in order to update and expand the knowledge of freshwater shrimp biodiversity in these lakes. In addition, we provide the first identification keys for the ancient lake species of Sulawesi, which are separated into one standard morphological key and two keys for the quick pre-identification of living specimens from each lake system. With the combination of morphological and molecular data, we further discuss the morphology-based species descriptions.

### MATERIAL AND METHODS

The study is based on material collected during several field trips to the ancient lakes of Sulawesi from 2002 to 2005 (Fig. 1C) by the authors, but also by M. Glaubrecht and T. von Rintelen (for collecting details compare the respective material examined section of each species). Species from the lakes were caught by hand net or with plastic containers while snorkelling or scuba diving; the riverine taxa only with hand nets. For scanning electron microscopy (SEM), specimens were fixed in 95% ethanol. All other specimens are preserved in 75% ethanol, if not otherwise indicated

as SEM material (mounted on specimen stubs). Voucher specimens are deposited in three museums: all holotypes, half of the paratype series, and approximately half of the non-type material at the Division of Zoology, Research Center for Biology, Indonesian Institute of Sciences (formerly Museum Zoologicum Bogoriense, MZB); approximately half of the paratype series and the remaining material at the Museum für Naturkunde Berlin (formerly Zoologisches Museum Berlin, ZMB), and some paratypes at the Zoological Reference Collection of the Raffles Museum for Biodiversity Research, National University of Singapore, Singapore (ZRC). In addition, we re-examined type specimens from the Natural History Museum Basel, Basel, Switzerland, (NHMB).

Digital photographs of the majority of living species from the ancient lakes were taken in a small fish tank directly after capture. The description of colour patterns is based on field notes and colour pictures taken from different angles (e.g. dorsal and lateral). Additional notes on substrate, behaviour, and ecology were taken whenever possible (rocks in shallow water generally refer to a depth above 3 m, rocks in deeper water to a depth below 3 m, if not otherwise indicated). A morphological overview with standard characters examined is provided in Fig. 2. Specimens and their qualitative characters were studied with a Leica MZ12 stereo microscope and a Zeiss Axioskop 20 light microscope in 75-95% ethanol. Some specimens of each species fixed in 95% ethanol were dehydrated in 100% ethanol for 30 minutes and afterwards critical point dried with a BAL-TEC CPD 030, mounted on aluminium specimen stubs with standard adhesive pads, and coated with gold-palladium using a Polaron SC7 640 Sputter Coater. SEM pictures were taken on a LEO 1450VP Scanning

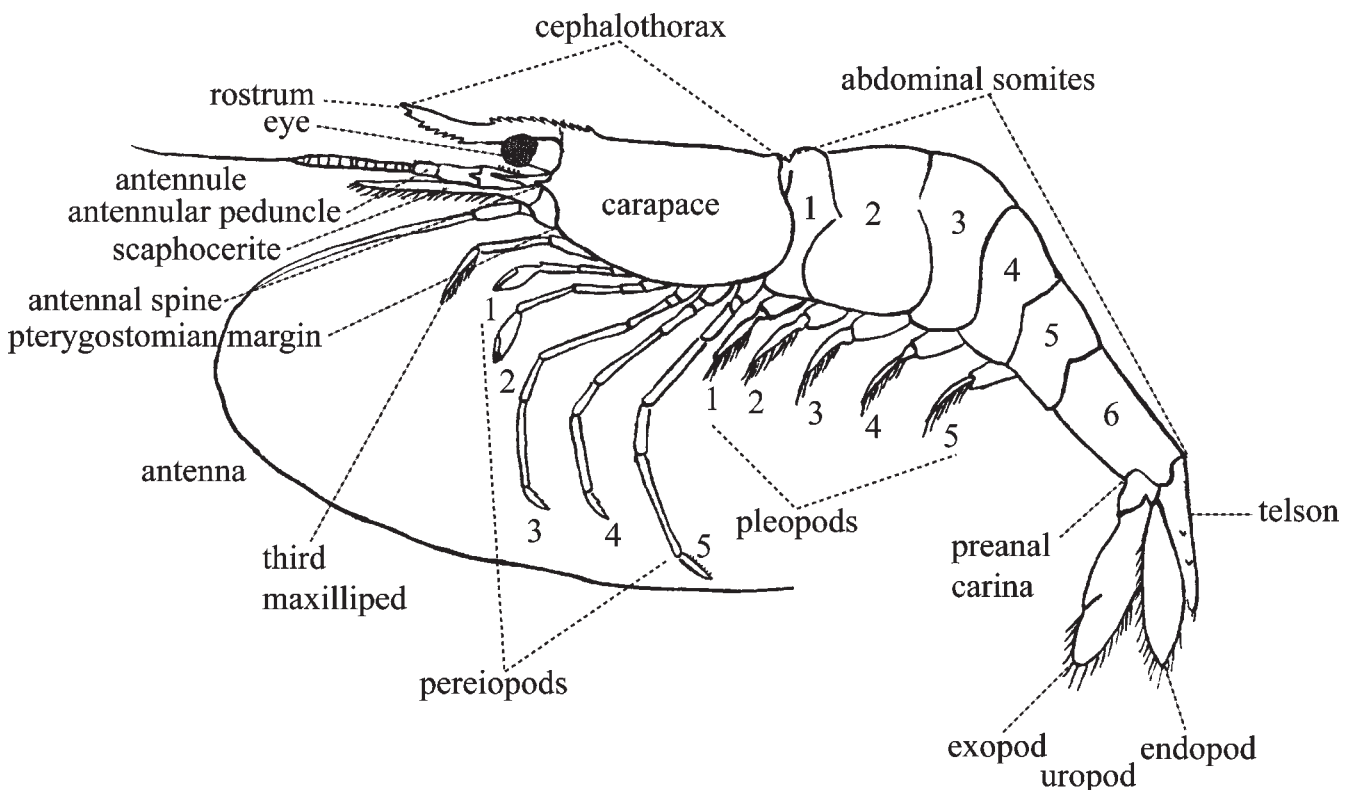


Fig. 2. General morphology of *Caridina* (modified from Holthuis, 1955: 3; shrimp drawing modified from Woltereck, 1937a: 215).

Electron Microscope (software: 32 V02.03) at 10 kV and later processed with Adobe Photoshop CS2. Morphometric measurements (for details and abbreviations see Fig. 3) were taken using a Leica MZ12 stereo microscope with an ocular micrometer. Standard descriptive statistical parameters (sample size, range, mean, and standard deviation (SD), median) were calculated using Microsoft Excel 2000. In species descriptions, mean and median were included. The median was considered as more meaningful in interspecific comparisons, because it relativizes outliers and thus better represents the average population parameter than the mean. Therefore, in the taxonomic remarks, the range and the median are compared between species, although in most cases mean and median were identical. Standard parameters have been taken as shown in Fig. 3. The width of the dactyli of the third and fifth pereiopod were measured without the spines on the flexor margin, because these were sometimes broken; the terminal spines were included in the measurements, but not in the spine counts. Drawings of dissected specimens were either made with a camera lucida mounted on the stereo microscope or a light microscope (for fragile body appendages, e.g. pleopods), or from SEM pictures (e.g. uropodal diaeresis, telson). Drawings were then digitized and processed with Adobe Photoshop and Illustrator CS2.

The connecting rivers within the Malili lake system, e.g. Tominanga River (Fig. 1C) are rather an extension of the lakes themselves (albeit with currents). Thus, in the material examined section, specimens of lake species found in the Petea and Tominanga rivers as well as specimens from Larona River close to the outlet bay of Lake Towuti (figure 1C) have been assigned to the lake into which the respective river is draining: Petea = Lake Matano; Tominanga = Lake Mahalona; Larona = Lake Towuti (compare von Rintelen et al., in review). For this study, over 4,600 adults (plus several juveniles) were examined. We thus abandoned to list the sex for the majority of specimens in the material examined section.

The molecular phylogeny (tree topology) of species of *Caridina* from the ancient lakes (and other species from Sulawesi and Java shown in Figs. 63-64 that are not part of this taxonomic revision) was taken from von Rintelen et al., (in review). However, species names were updated for this study, and here, the molecular results for each species are discussed in the respective taxonomic remark section following each species description (for technical details and sequence accession numbers see von Rintelen et al., in review).

**REVISION OF CARIDINA FROM THE ANCIENT LAKES OF SULAWESI**

In this revision, 21 species are recognized from the ancient lakes of Sulawesi, 15 (including eight new taxa) from the Malili lakes and six (including two new taxa) from Lake Poso (Tables 2-3); details of each species are provided below.

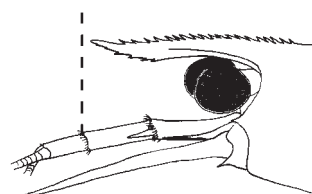
**Identification keys to species from the ancient lakes of Sulawesi.** – Woltereck (1937a, b) mentioned the rostrum as a good character to delimit the different species she described from the Malili lakes: “...the rostrum varies in length, but the type does not change.” (Woltereck, 1937a: 228). Schenkel (1902) provided a detailed description of the rostrum in species from Lake Poso and included an elaborate table of rostral characters from one species. The recent examination of specimens from both lake systems confirmed that shape and denticulation of the rostrum are constant in the majority of the species. Therefore, the following morphological key is mainly based on rostral characters from adult specimens of both sexes (although it has to be mentioned that females are generally larger than males). It is not appropriate for the identification of most juveniles, though.

During sampling in the lakes, most species could easily be told apart (juveniles included) based on colour pattern, substrate, collecting site, or behaviour. Thus, an additional key for each lake system is provided for the quick pre-identification of living animals in the field. Because each species flock is endemic to its respective lake system and both lake systems are completely isolated from each other, the key to living animals in the field is subdivided into species from the Malili lake system and from Lake Poso (and its river system).

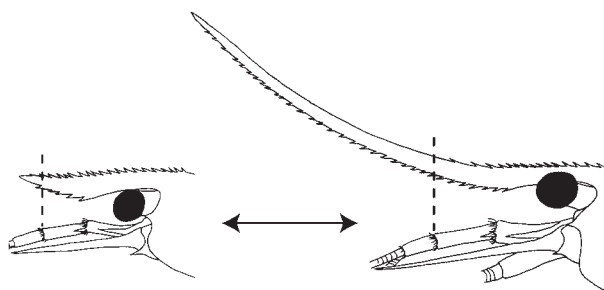
All keys provided here are only applicable to species of *Caridina* from the ancient lakes of Sulawesi.

**MORPHOLOGICAL KEY TO ALL ANCIENT LAKE SPECIES**

- 1 Rostrum distinctly shorter than scaphocerite and antennular peduncle (maximal reaching to end of second segment) ... 2



- Rostrum longer (overreaching second segment of antennular peduncle), reaching near to or beyond end of scaphocerite or antennular peduncle ..... 5



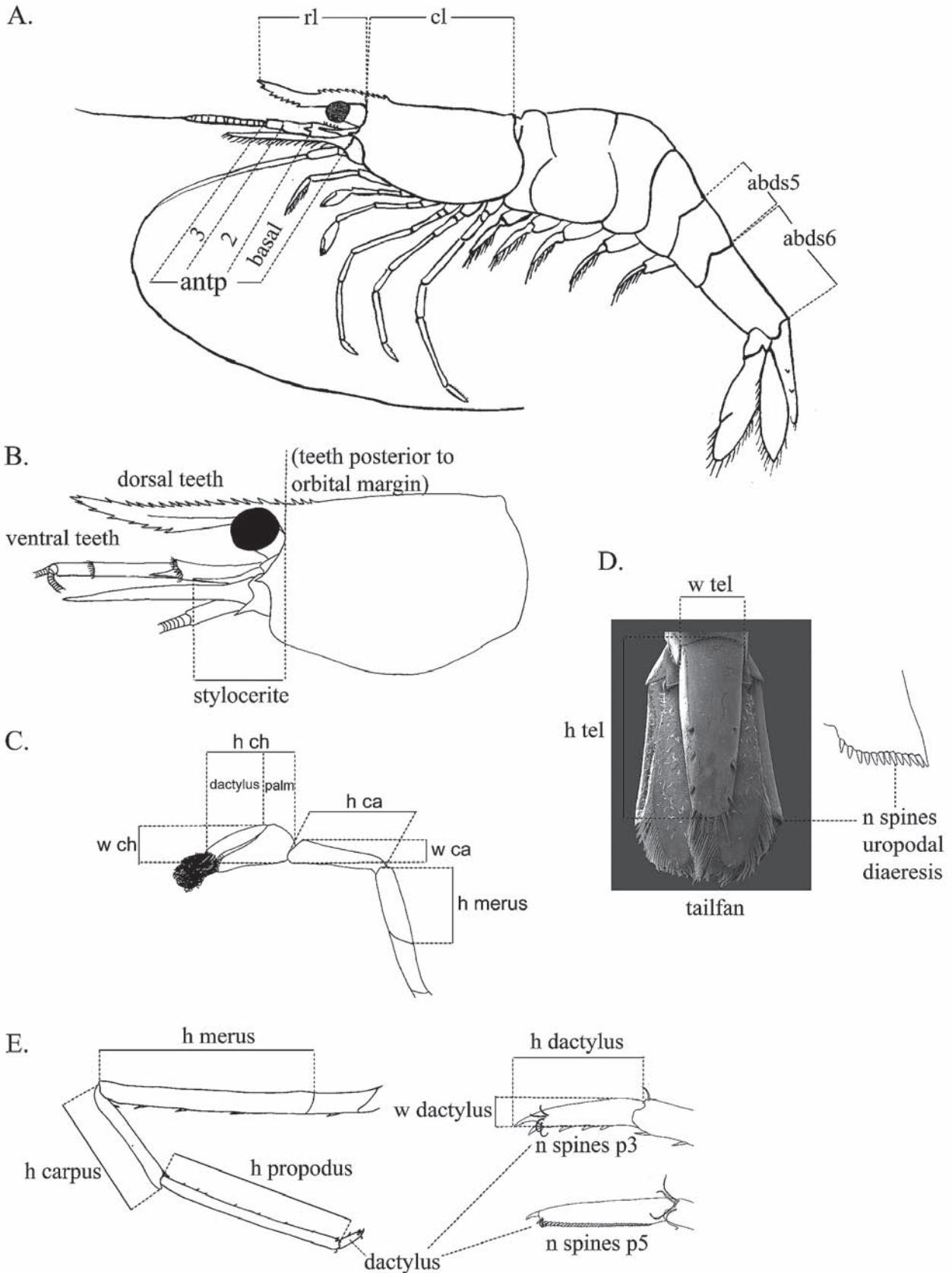


Fig. 3. Standard morphometric characters in *Caridina*. A. Cephalothorax and abdomen (shrimp drawing modified from Woltereck, 1937a: 215). B. Rostrum and cephalic appendages. C. First and second pereiopod. D. Tailfan (telson and uropods). E. Third and fifth pereiopod. Abbreviations. antp (length of antennular peduncle), cl (carapace length), rl (rostrum length), abds5 (length of fifth abdominal somite), abds6 (length of sixth abdominal somite), h tel (length/height of telson), w tel (width of telson), h ch1 (length/height of chela of first pereiopod), w ch1 (width of chela of first pereiopod), h ca1 (length/height of carpus of first pereiopod), w ca1 (width of carpus of first pereiopod), h ch2 (length/height of chela of second pereiopod), w ch2 (width of chela of second pereiopod), h ca2 (length/height of carpus of second pereiopod), w ca2 (width of carpus of second pereiopod), n spines p3 (number of spines on the dactylus of the third pereiopod), n spines p5 (number of spines on the dactylus of the fifth pereiopod).

Table 1. Current taxonomy of species from the ancient lakes of Sulawesi based on this revision (in alphabetical order).

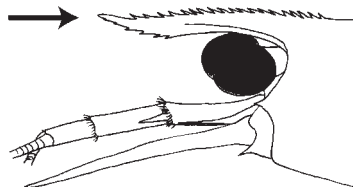
Taxon	Lake system	State of endemism	Remarks
<i>C. acutirostris</i> Schenkel, 1902	Poso	endemic	riverine (generalist?)
<i>C. caerulea</i> , new species	Poso	endemic	lacustrine (specialist?)
<i>C. dennerli</i> , new species	Malili	endemic	lacustrine specialist
<i>C. ensifera</i> Schenkel, 1902	Poso	endemic	lacustrine generalist
<i>C. glaubrechtii</i> , new species	Malili	endemic	lacustrine specialist
<i>C. holthuisi</i> , new species	Malili	endemic	lacustrine specialist
<i>C. lanceolata</i> Woltereck, 1937a	Malili	endemic	lacustrine generalist
<i>C. lingkonae</i> Woltereck, 1937a	Malili	endemic	lacustrine specialist
<i>C. loehae</i> Woltereck, 1937a	Malili	endemic	lacustrine specialist
<i>C. longidigita</i> Cai & Wowor, 2007	Poso	endemic	lacustrine specialist
<i>C. mahalona</i> Cai et al., 2009	Malili and Tomori area	non-endemic	riverine generalist
<i>C. masapi</i> Woltereck, 1937a	Malili	endemic	riverine generalist
<i>C. parvula</i> , new species	Malili	endemic	lacustrine specialist
<i>C. profundicola</i> , new species	Malili	endemic	lacustrine specialist
<i>C. sarasinorum</i> Schenkel, 1902	Poso	endemic	lacustrine (specialist?)
<i>C. schenkeli</i> , new species	Poso	endemic	riverine generalist
<i>C. spinata</i> Woltereck, 1937a	Malili	endemic	lacustrine specialist
<i>C. spongicola</i> Zitzler & Cai, 2006	Malili	endemic	lacustrine specialist
<i>C. striata</i> , new species	Malili	endemic	lacustrine specialist
<i>C. tenuirostris</i> Woltereck, 1937a	Malili	endemic	lacustrine specialist
<i>C. woltereckae</i> Cai et al., 2009	Malili	endemic	lacustrine specialist

Table 2. Comparison of species diversity in both lake systems after a taxonomic revision.

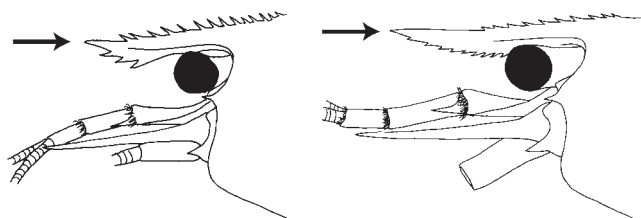
Lake system	n species before revision	n species after revision
Poso system	4	6
Malili lake system	10*	15
Total	14	21

\*including *Caridina towutensis* Woltereck, 1937a.

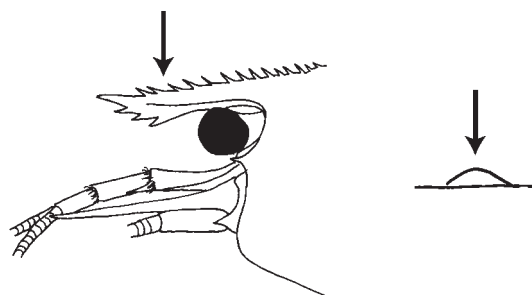
2 Rostrum slender and appearing fragile, body small (carapace length < 3.0 mm), number of spines on the dactylus of the fifth pereiopod < 20 ..... *C. loehae*



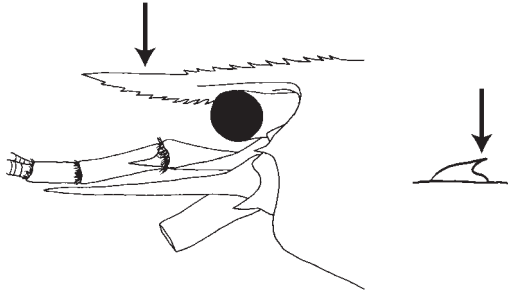
– Rostrum appearing rather broad and robust, teeth usually pronounced, number of spines on the dactylus of the fifth pereiopod > 30 ..... 3



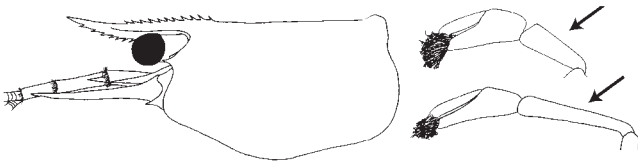
3 Body usually small (mean carapace length < 3.0 mm), rostrum never reaching to end of second segment of antennular peduncle, without a conspicuous gap on the dorsal margin, preanal carina rounded, without a spine ..... *C. parvula*



- Body usually large (mean carapace length > 4 mm), rostrum can reach second segment of antennular peduncle, with a conspicuous unarmed gap on the dorsal margin, preanal carina with a spine ..... 4

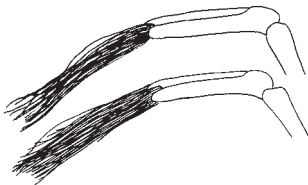


- 4 Rostrum reaching near or to end of second segment of antennular peduncle, scaphocerite rather stout (3.0–3.6 times as long as wide), carpus of first and second pereiopod stouter (2.0–2.7 and 4.5–5.9 times as long as wide), Poso riverine species ..... *C. acutirostris*

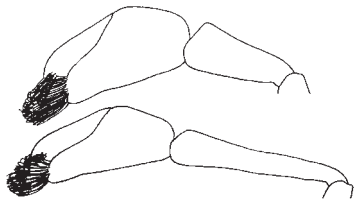


- Rostrum length variable, reaching to end of second segment of antennular peduncle or distinctly shorter, scaphocerite rather slender (3.5–4.1 times as long as wide), carpus of first and second pereiopod more slender (2.5–3.3 and 5.6–7.0 times as long as wide), Malili riverine species ..... *C. mahalona*

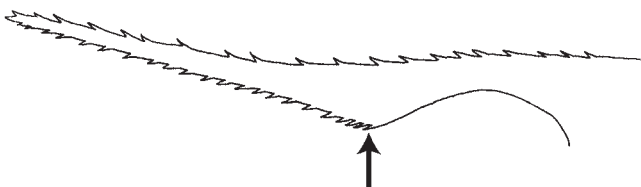
- 5 Chelae of first and second pereiopod uniformly long and slender, bearing very long fingers (setae), about as long as chelae ..... *C. longidigita*



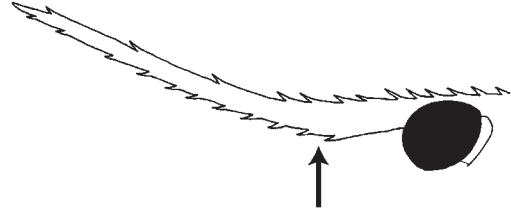
- Chelae of first and second pereiopod not uniformly long and slender, fingers rather short ..... 6



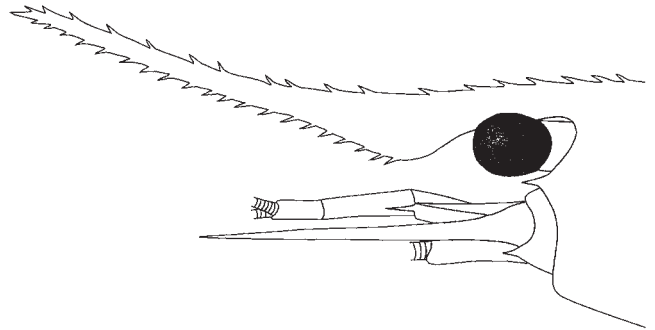
- 6 Proximal part of rostrum conspicuously triangular (best visible transilluminated), otherwise more slender, dorsal denticulation without unarmed gap, first and second pereiopod very slender ..... 7



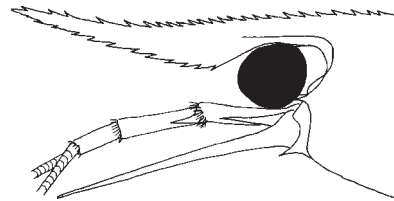
- Proximal part of rostrum not conspicuously triangular, with or without unarmed gap on dorsal margin, first and second pereiopod stout to slender (if very slender, then rostrum slender throughout) ..... 8



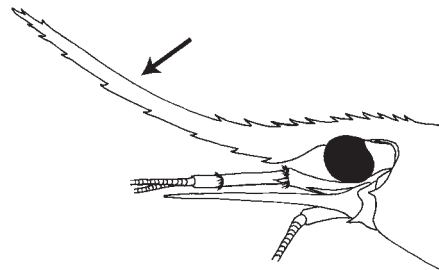
- 7 Rostrum very long, reaching far beyond end of scaphocerite (ratio rostrum length/carapace length 1.4–2.8), distal part very slender ..... *C. profundicola*



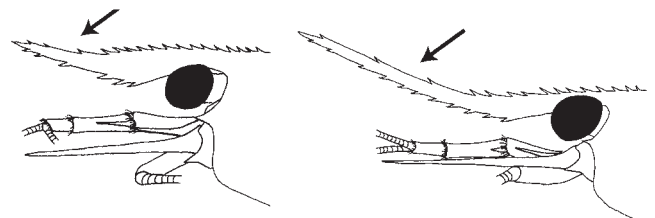
- Rostrum reaching beyond end of scaphocerite (ratio rostrum length/carapace length 1.0–1.6), but not very far, generally broader and stouter ..... *C. lingkonae*



- 8 Rostrum with a conspicuous unarmed gap on the dorsal margin, distally completely unarmed or with few widely spaced teeth, with or without subapical teeth ..... 9

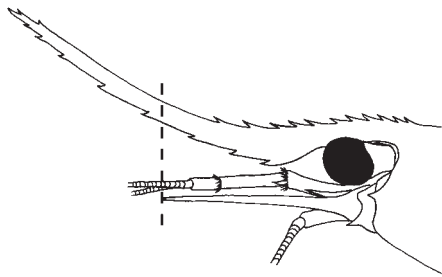


- Dorsal margin of rostrum without a conspicuous unarmed gap, denticulation throughout, although sometimes distally less densely spaced ..... 15

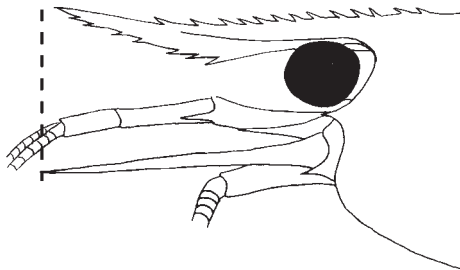




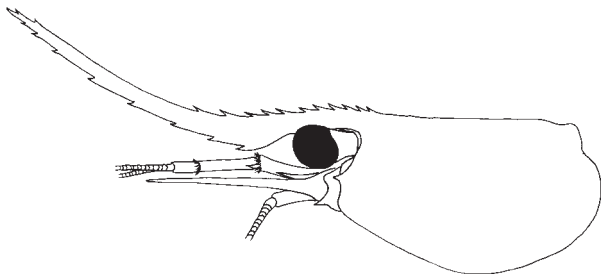
- 9 Rostrum reaching well beyond end of scaphocerite (ratio rostrum length/carapace length >1.1) ..... 10



- Rostrum reaching near to or slightly beyond end of scaphocerite (ratio rostrum length/carapace length <1.1) ..... 14

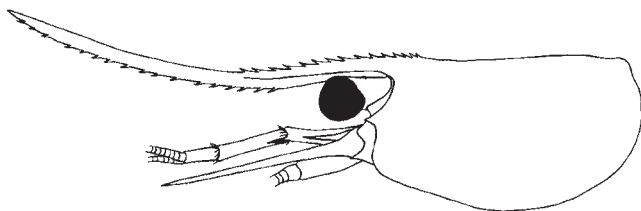


- 10 Rostrum strongly upturned, usually with 1-4 subapical teeth, ventral teeth prominent and widely spaced, sixth abdominal somite long (0.8-1.1 times length of carapace) .....  
..... *C. lanceolata*



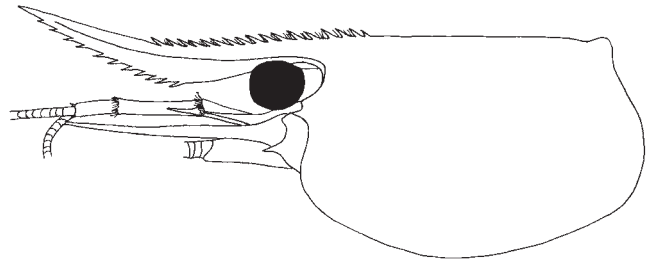
- Rostrum straight to upturned (if strongly upturned ventral teeth densely spaced), but always without subapical teeth, sixth abdominal somite shorter (max. 0.8-0.9 times length of carapace) ..... 11

- 11 Rostrum very slender, body small and slender (carapace length 2.4-3.3 mm), about 3 spines on the dactylus of the third and 11-15 spines on the dactylus of the fifth pereiopod, Malili species ..... *C. tenuirostris*

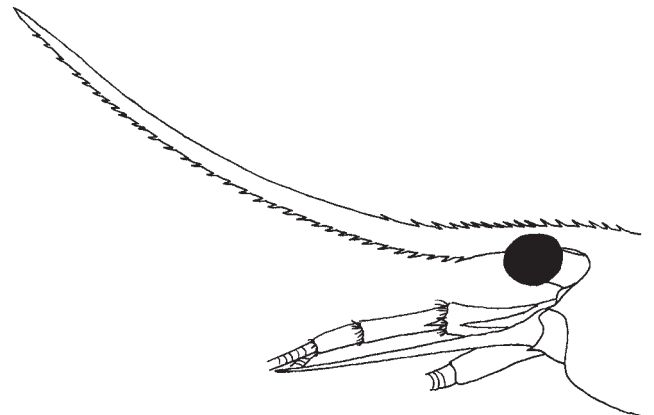


- Rostrum broad to slender, body usually distinctly larger or more robust (carapace length 2.6-5.3 mm), about 4-9 spines on the dactylus of the third and >30 spines on the dactylus of the fifth pereiopod, Poso species ..... 12

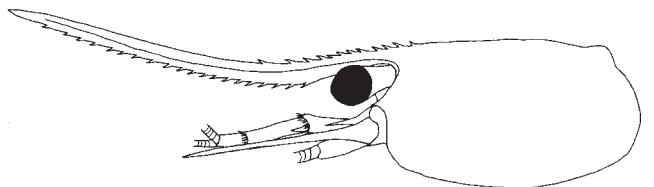
- 12 Rostrum not extremely long and slender (ratio rostrum length/carapace length 1.0-1.2), number of ventral teeth 8-14 .....  
..... *C. sarasinorum*



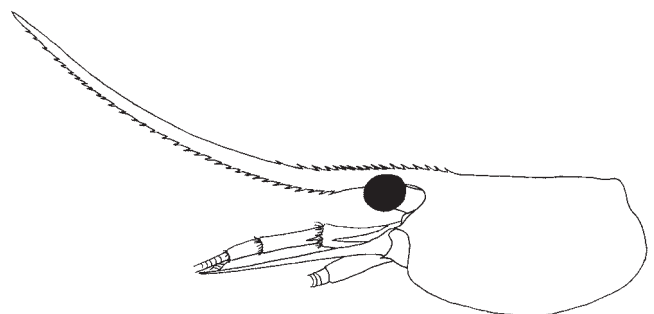
- Rostrum extremely long and slender (ratio rostrum length/carapace length >1.4), 16-48 ventral teeth ..... 13



- 13 Rostrum with distinctly less teeth (dorsal 9-15, ventral 16-29) and shorter compared to carapace length (1.4-2.3), uropodal diaeresis with 9-11 spines, 6-9 spines on the dactylus of the third and 51-57 spines on the dactylus of the fifth pereiopod ..... *C. ensifera*



- Rostrum with distinctly more teeth (dorsal 11-20, ventral 26-48) and longer compared to carapace length (1.9-2.6), uropodal diaeresis with 11-14 spines, 4-5 spines on the dactylus of the third and 27-49 spines on the dactylus of the fifth pereiopod ..... *C. caerulea*



- 14 Malili (typical riverine) species .... *C. masapi*, *C. Mahalona*  
- Poso (typical riverine) species .. *C. acutirostris*, *C. schenkeli*

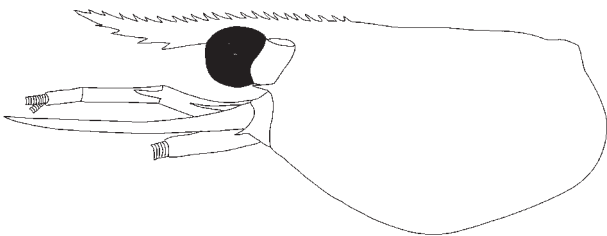
15 Preanal carina rounded, without a spine ..... 16



– Preanal carina with a spine ..... 17

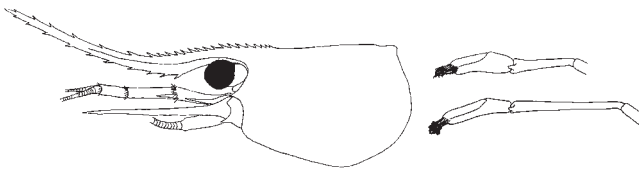


16 Rostrum not overreaching scaphocerite or antennular peduncle, body small (carapace length 1.8–2.8 mm) ..... *C. spongicola*



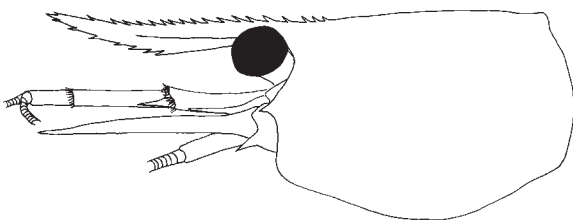
– Rostrum reaching (slightly) beyond end of scaphocerite and antennular peduncle, carapace length 2.8 mm or more .....  
..... *C. striata*, *C. glaubrechtii*, *C. woltereckae*

17 Rostrum long, reaching beyond end of scaphocerite, first and second pereiopod conspicuously slender ..... *C. spinata*

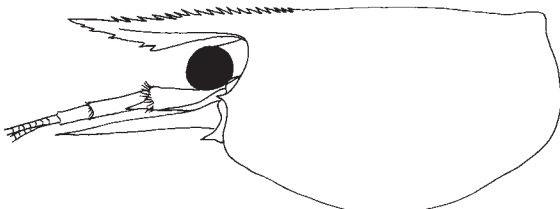


– Rostrum reaching near or slightly beyond end of scaphocerite, first and second pereiopod not conspicuously slender ..... 18

18 Rostrum completely lacking a dorsal gap, slightly falciform, about 2 spines on the dactylus of the third and 25–30 spines on the dactylus of the fifth pereiopod, Lake Matano species ..... *C. dennerli*

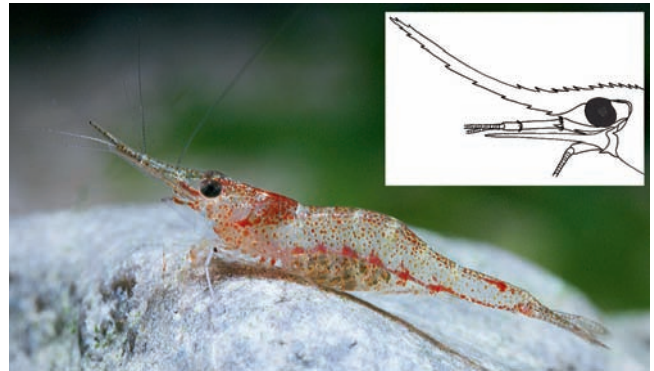


– Rostrum often with an inconspicuous unarmed gap on dorsal margin (less than ¼ of total length), the shape rather straight or angular, 3–6 spines on the dactylus of the third and 27–39 spines on the dactylus of the fifth pereiopod ..... *C. holthuisi*

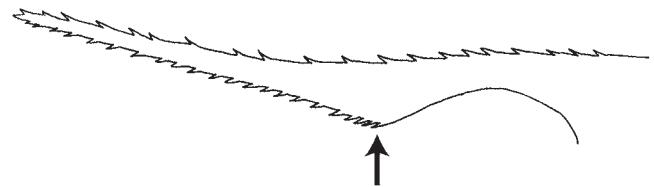


**KEY TO LIVING ANIMALS IN THE FIELD  
(MALILI LAKE SYSTEM)**

- 1 Body reddish or yellowish, but mainly translucent ..... 2
- Body colour red or brown, often with white or beige markings ..... 3
- 2 Rostrum longer than scaphocerite and strongly upturned, with prominent teeth and a conspicuous unarmed gap on dorsal margin, without a triangular shape, body yellowish to reddish, movements in all directions, from lakes or rivers .....  
..... *C. lanceolata*



- Proximal part of rostrum conspicuously triangular, first and second pereiopod extremely slender, from Lake Towuti or Lake Mahalona ..... 4



- 3 Collected from Lake Masapi or Lake Lontoa ..... *C. masapi*
- Collected from other localities ..... 5
- 4 Rostrum very long, reaching far beyond end of scaphocerite, body large and yellowish, abdomen with few yellow stripes, sometimes a kind of green saddle visible, eggs of ovigerous females green, keeps rather still when disturbed, movements side- or downwards, usually between large boulders below 3 m, juveniles also on other substrate, only from Lake Towuti .....  
..... *C. profundicola*



- Rostrum distinctly shorter, can overreach scaphocerite, but not very far, body usually reddish, pelagic or on substrate, but usually in shallow water, movements in all directions, in Lake Towuti or Lake Mahalona ..... *C. lingkonae*



- 5 Body crimson to deep red with orange or yellow appendages, often with two to three yellow or orange transversal stripes and a few same coloured dots on various body parts, antennules white, colours appearing bright and vivid, on rocks, often between boulders below 3 m, only from Lake Towuti .....  
..... *C. spinata*



- Body not red or if dark red, then without a conspicuous combination of yellow or orange, usually not between boulders below 3 m ..... 6
- 6 Body bright to dark red, colour vivid, either without white markings, with white dots or dorsally with small transversal stripes, but without conspicuous stripes, on rocks ..... 7
- Body usually not unicoloured, but with conspicuous bands or longitudinal stripes ..... 8
- 7 Body always red covered with white dots, one distinct dot on the dorsodistal part of the abdomen, chela and carpus of the first and second pereopod bright white, antenna, antennules and scaphocerite white, only in Lake Matano .... *C. dennerli*



- Body red, but without conspicuous white dots, on rocks in shallow water ..... 9

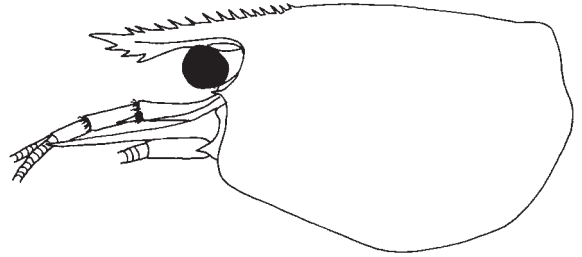
- 8 Body mainly brown and white (harlequin-like), on sponges in the outlet bay of Lake Towuti (fits in the sponges' cavities) ..... *C. spongicola*



- Body either with a similar pattern, but then larger and mainly on rocks, or with a different colour pattern ..... 10
- 9 Body red with white bands, tips of uropods white, rostrum slender ..... *C. loehae*



- Body only red, rostrum stouter ..... *C. parvula*



- 10 Body red, lateral with several longitudinal white stripes, first and second pereopod partly conspicuously white, on rocks in Lake Towuti or Lake Mahalona ..... *C. striata*



- Body colouration with a different pattern ..... 11

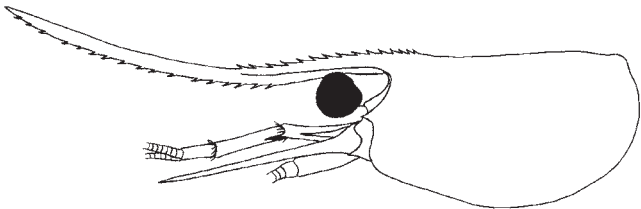
- 11 Body large, with the harlequin pattern similar to *C. spongicola*, on rocks, only in Lake Towuti ..... *C. woltreckae*



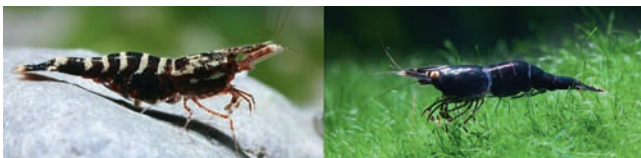
- Body colouration with a different pattern ..... 12  
 12 Body mainly brown with several white bands, on rocks, only in Lake Towuti ..... 13  
 – Body colouration with a different pattern ..... 14  
 13 Rostrum without a conspicuous gap on dorsal margin, only in Lake Towuti, collected from rocks ..... *C. glaubrechtii*



- Rostrum with a conspicuous gap on dorsal margin, in Lake Towuti, Lake Mahalona and Tominanga River, collected from wood ..... *C. tenuirostris*

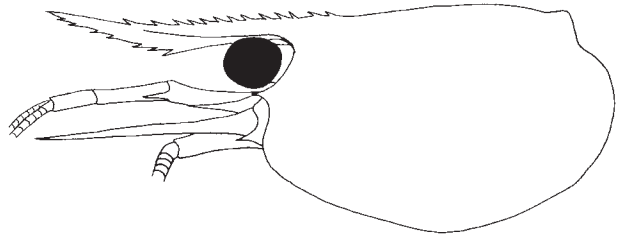


- 14 Body dark brown, colour vivid, either completely without or with white-beige markings, rostrum straight and broad usually under leaf litter, mainly in the lakes ..... *C. holthuisi*



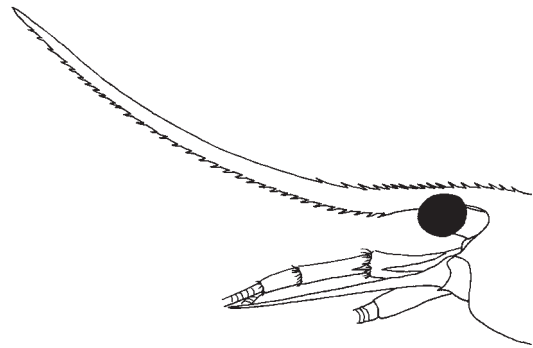
- Body less vivid brown or otherwise coloured, rostrum usually more slender and slightly curved, occurring in rivers or lakes ..... 15

- 15 Body usually larger and more robust, rostrum highly variable, only occurring in rivers ..... *C. mahalona*  
 – Body usually smaller and less robust, rostrum reaching to or slightly beyond end of scaphocerite, occurring in rivers and lakes ..... *C. masapi*

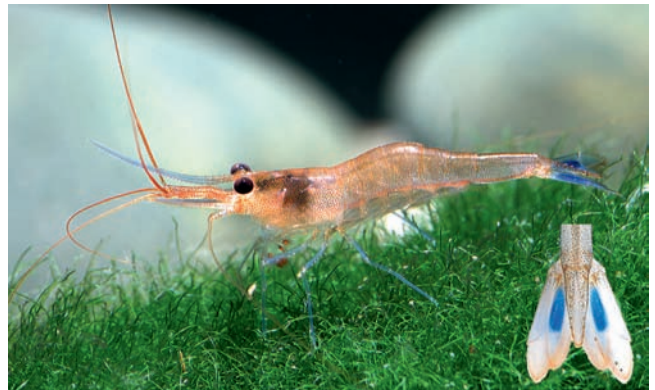


**KEY TO LIVING ANIMALS IN THE FIELD  
(LAKE POSO AND ITS RIVER SYSTEM)**

- 1 Rostrum conspicuously long and slender (reaching far beyond end of scaphocerite), body also slender and mainly transparent, appendages bluish or reddish, uropods with clearly visible red or blue spots, often in huge swarms or attached to a substrate, collected from the lake ..... 2



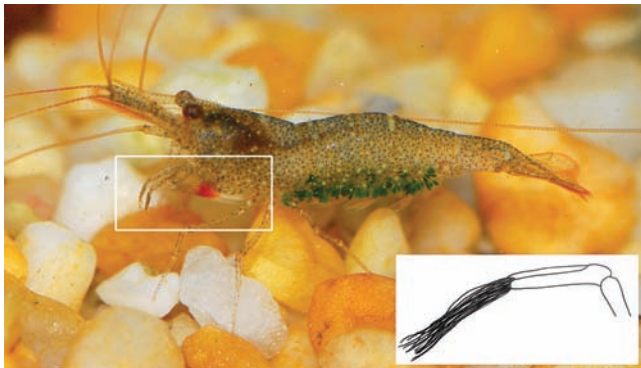
- Rostrum short to long, but not conspicuously long, body usually more robust and less transparent, usually attached to any kind of substrate, collected from the lake or rivers ..... 3  
 2 Main colour of appendages bluish, tailfan with two conspicuous blue patches on each uropods ..... *C. caerulea*



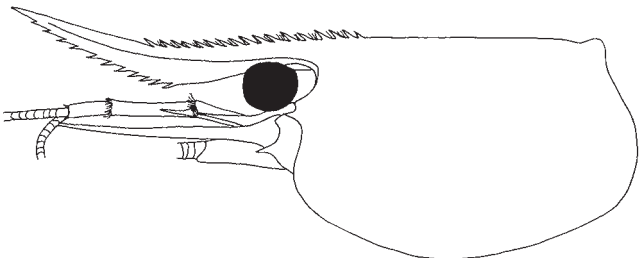
- Main colour of appendages reddish, not bluish, tailfan with two conspicuous red patches on distal part of each uropods ..... *C. ensifera*



- 3 First and second pereiopod with conspicuously long chelae and fingers (setae), fingers partly orange, body brownish to greenish, usually on rocks or wood (hard substrate), rostrum longer than scaphocerite, collected from the lake ..... *C. longidigita*



- First and second pereiopod without conspicuously long fingers, collected from the lake or from rivers ..... 4
- 4 Rostrum reaching well beyond end of scaphocerite, first and second pereiopod rather stout, collected from the lake ..... *C. sarasinorum*



- Rostrum shorter, reaching slightly beyond end of scaphocerite, first and second pereiopod not conspicuously stout, from rivers ..... *C. acutirostris*, *C. schenkeli*

**TAXONOMY**

**ATYIDAE de Haan, 1849**

***Caridina* H. Milne Edwards, 1837**

*Caridina* H. Milne Edwards, 1837: 362.

**Type species.** – *Caridina typus* H. Milne Edwards, 1837: 363 (type locality unknown, gender feminine), by monotypy.

**SPECIES FROM THE MALILI LAKE SYSTEM (INDONESIA, SOUTH SULAWESI)**

***Caridina dennerli*, new species**  
(Figs. 4-6; Table 3)

**Material examined.** – Holotype: ovigerous female (cl 3.1 mm)(MZB Cru 1540), Lake Matano, east shore, just at entrance to outlet bay, 02°31.54'S, 121°27.00'E, loc. 43-03, on gravel in shallow water, coll. K. & T. von Rintelen, 18 Sep.2003.

Paratypes (all Lake Matano) – 24 ex. (MZB Cru 1542, n=10; ZMB 29024, n=14, some SEM material), south shore, Soroako, Salonsa, INCO boat house, 02°30.71'S, 121°20.45'E, loc. 19-03, on gravel in shallow water, coll. K. & T. von Rintelen, 19 Sep.2003; 24 ex. (MZB Cru 1541, n=14 and ZMB 29049, n=10, some SEM material), east shore, just at entrance to outlet bay, 02°31.54'S, 121°27.00'E, loc. 43-03, on gravel in shallow water, coll. K. & T. von Rintelen, 18 Sep.2003; 9 ex. (MZB Cru 1548, n=4; ZMB 29050, n=5, some SEM material), north shore, 02°27.28'S, 121°21.21'E, loc. 98-03, on gravel, coll. K. & T. von Rintelen, 1 Oct.2003; 25 ex. (MZB Cru 1544, n=13; ZMB 29051, n=12, some SEM material), northwest corner, 02°27.71'S, 121°13.03'E, loc. 102-03, on boulders in deeper water, coll. K. & T. von Rintelen, 1 Oct.2003; 9 ex. (MZB Cru 1546, n=5; ZMB 29103, n=4, some SEM material), east shore, south bay, 02°32.77'S, 121°26.71'E, loc. 45-03, on gravel, coll. K. & T. von Rintelen, 1 Oct.2003; 10 ex. (MZB Cru 1547, n=5; ZMB 29104, n=5 and few juveniles, some SEM material), southwest shore, Cape Nikomene, 02°32.24'S, 121°24.76'E, loc. 46-03, on gravel, coll. K. & T. von Rintelen, 1 Oct.2003; 3 ex. (ZMB 29153, n=3 and few juveniles), south shore, near cave entrance, 02°29.85'S, 121°18.66'E, loc. 60-03, on boulders in deeper water, coll. K. & T. von Rintelen, 24 Sep.2003; 3 ex. (ZMB 29155), south shore, 02°27.84'S, 121°13.88'E, loc. 63-03, on gravel, coll. K. & T. von Rintelen, 24 Sep.2003; 3 ex. (ZMB 29156, some SEM material), north shore, 02°25.67'S, 121°16.54'E, loc. 65-03, on gravel, coll. K. & T. von Rintelen, 25 Sep.2003; 4 ex. (ZMB 29157), north shore, 02°26.36'S, 121°19.03'E, loc. 84-03, on gravel, coll. K. & T. von Rintelen, 1 Oct.2003; 14 ex. (MZB Cru 1545, n=7; ZMB 29326, n=7, some SEM material), south shore, 02°27.85'S, 121°13.87'E, loc. 125-04, on boulders in deeper water, coll. P. Koller & K. von Rintelen, 1 Aug.2004; 1 ex. (ZMB 29327), south shore, canal between island and mainland, 02°28.46'S, 121°15.83'E, loc. 62-03, on gravel, coll. K. & T. von Rintelen, 1 Oct.2003; 3 ex. (ZMB 29328), north shore, 02°26.274'S, 121°18.83'E, loc. 133-04, on gravel, coll. K. & T. von Rintelen, 22 Jul.2004; 1 ex. (ZMB 29329), west shore, 02°26.828'S, 121°12.988'E, loc. 135-04, on gravel, coll. K. & T. von Rintelen, 23 Jul.2004; 3 ex. (ZMB 29330), north shore, 02°27.311'S, 121°21.047'E, loc. 09-05, on gravel in shallow water, coll. K. & T. von Rintelen, 7 Jan.2005; 4 ex. (MZB Cru 1543), Lake Matano (no details given), loc. F2-02, substrate unknown, coll. F. Herder & A. Nolte, 1 Dec.2002.

**Description.** – Carapace length 1.5-3.4 mm (n=53). Rostrum (Fig. 5A; Table 3) reaching near or to end of scaphocerite, slightly sickle-shaped, 0.9-1.3 times as long as carapace (n=39), armed dorsally with 15-25 teeth (including 3-7 teeth posterior to orbital margin), anterior less densely spaced, armed ventrally with 5-11 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.5 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 1.0-1.3 times as long as carapace (n=5), second segment 2.0-2.2 times length of third segment, third segment

0.3-0.4 times length of basal segment. Stylocerite reaching 0.8-0.9 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 5D) 4.3-5.7 times as long as wide (n=5).

Sixth abdominal somite 0.5-0.7 times length of carapace (n=35), 1.4-2.0 times as long as fifth somite (n=32), 0.8-1.0 times length of telson (n=24). Telson (Fig. 5C,H) 3.1-3.3 times as long as wide (n=5), distal margin rounded, without projection, with 3-4 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 3-4 pairs of spines, lateral pair distinctly longer than intermediate pairs, median pair shortest. Preanal carina (Fig. 5E) with a spine. Uropodal diaeresis (Fig. 5B) with 12-13 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipod present on first pereopod, but reduced. Incisor process of mandible (Fig. 6A) ending in a row of 3-4 small teeth, molar process truncated. Lower lacinia of

maxillula (Fig. 6B) broadly rounded, upper lacinia elongate, with numerous distinct teeth and setae on inner margin, palp slender. Upper endites of maxilla (Fig. 6C) subdivided, palp elongated, scaphognathite tapering posteriorly with numerous long, curved setae at posterior end. Distal end of palp of first maxilliped (Fig. 6F) triangular, with a long finger-like projection; flagellum of the exopod very elongated, endopod high, reaching to half the flagellum of exopod in length. Second maxilliped (Fig. 6D) typical. Third maxilliped (Fig. 6E) with ultimate segment slightly shorter than penultimate segment.

First and second pereopod very slender, chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig. 5M-P); chela of first pereopod 2.4-3.8 times as long as wide (n=35), 0.9-1.1 times length of carpus (n=39); tips of fingers rounded, without hooks; dactylus 1.7-2.4 times as long as palm (n=6); carpus 3.3-4.6 times as long as wide (n=35), 1.4-1.8 times length of merus (n=5). Chela of second pereopod 2.8-3.7 times as long as wide (n=35), 0.6-0.7 times length of carpus (n=39); tips of fingers rounded, without hooks, dactylus 1.6-2.1 times

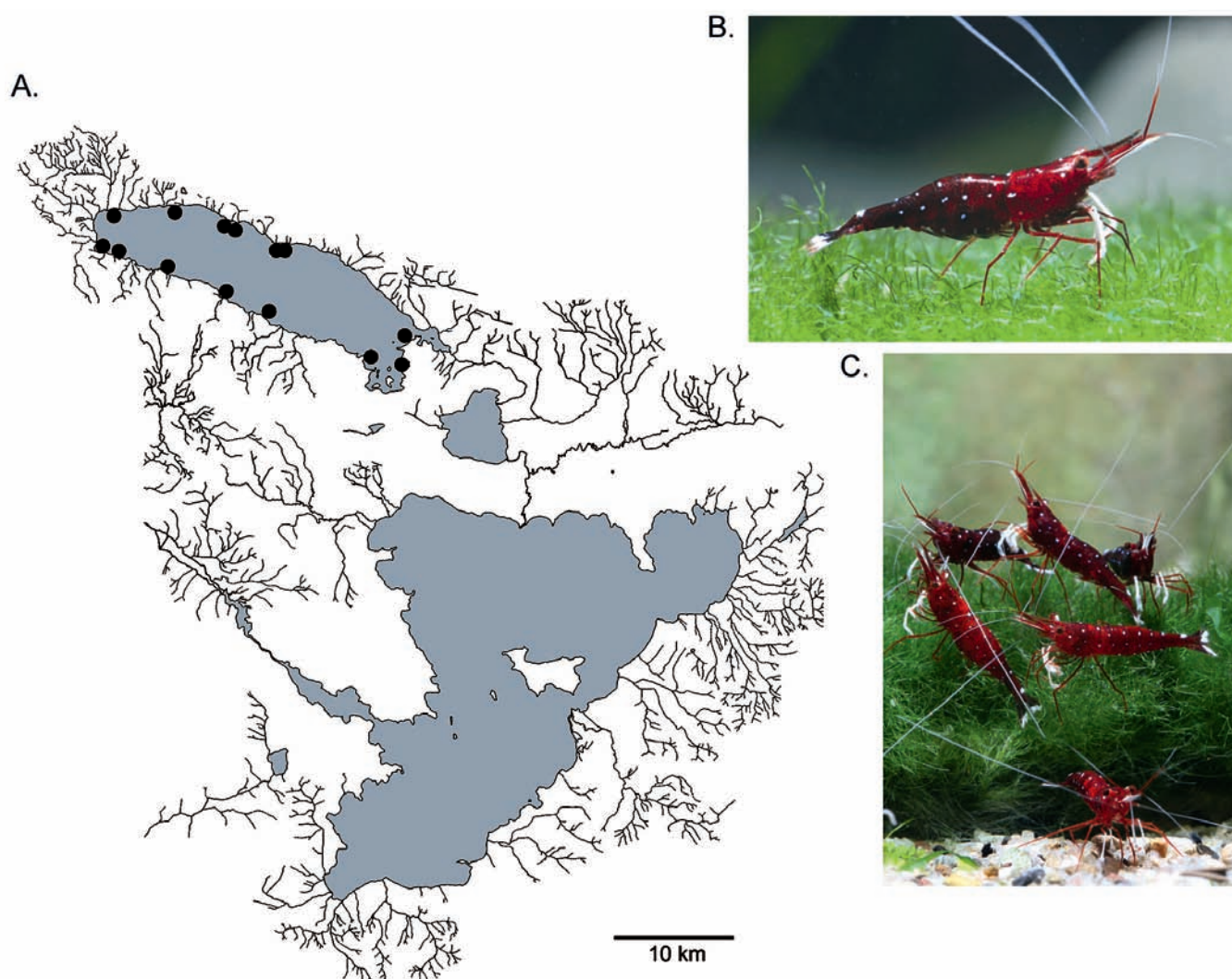


Fig. 4. *Caridina dennerli* from the Malili lake system. A. Distribution. B.-C. Colour pattern of living animals (not to scale). Pictures courtesy of Chris Lukhaup.

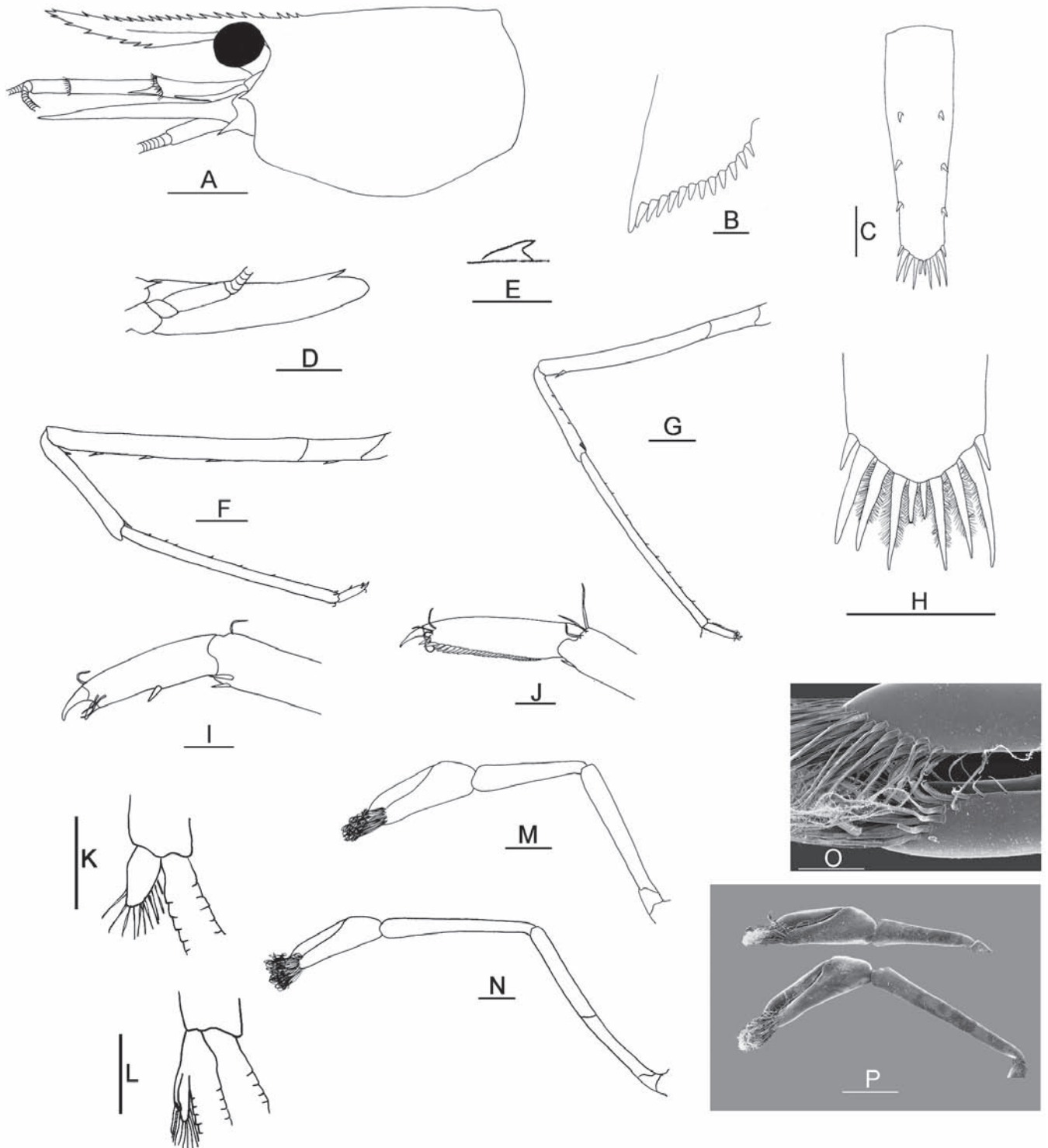


Fig. 5. *Caridina dennerli* from the Malili lake system. A. Cephalothorax and cephalic appendages, female (ZMB 29049); B. Uropodal diaeresis, male (ZMB 29051); C. Telson, male (ZMB 29156); D. Scaphocerite, male (ZMB 29051); E. Preanal carina, F. Third pereiopod, female (ZMB 29326); G. Fifth pereiopod; H. Distal end of telson male (ZMB 29156); I. Dactylus of third pereiopod female (ZMB 29326); J. Dactylus of fifth pereiopod; K. Endopod of male first pleopod (ZMB 29051); L. Appendix masculina of male second pleopod; M. First pereiopod, male (ZMB 29156); N. Second pereiopod; O. SEM image of anterior part of chela, male (ZMB 29104); P. SEM image of chela and carpus of first and second pereiopods, female (ZMB 29024). Scale bars: A, D = 1.0 mm; C, E-G, K-P = 0.5 mm; B, H-J = 0.1 mm.

Table 3. Summary of standard morphometric parameters for *Caridina dennerli*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	2.3-3.8	2.8 $\pm$ 0.4	2.7	29
rl / cl	0.6-1.2	0.9 $\pm$ 0.1	0.9	32
n dorsal rostral teeth	14-28	20 $\pm$ 3	20	32
n ventral rostral teeth	3-7	5 $\pm$ 1	5	32
abds6 / cl	0.5-0.7	0.6 $\pm$ 0.1	0.6	15
abds6 / abds5	1.4-1.8	1.6 $\pm$ 0.1	1.6	15
abds6 / h tel	0.9-1.0	0.9 $\pm$ 0.0	0.9	10
h tel / w tel	2.9-3.5	3.3 $\pm$ 0.2	3.4	6
n spines uropodal diaeresis	12-13	13 $\pm$ 1	13	5
h ch1 / w ch1	1.8-2.3	2.1 $\pm$ 0.2	2.1	18
h ch1 / h ca1	1.1-1.4	1.2 $\pm$ 0.1	1.2	17
h ca1 / w ca1	2.0-3.1	2.7 $\pm$ 0.3	2.7	13
h ch2 / w ch2	2.3-3.5	2.8 $\pm$ 0.3	2.8	18
h ch2 / h ca2	0.7-0.9	0.8 $\pm$ 0.1	0.7	22
h ca2 / w ca2	4.3-7.0	5.7 $\pm$ 0.9	5.7	18
n spines p3	3-6	4 $\pm$ 1	4	5
n spines p5	27-39	34 $\pm$ 5	33	5

as long as palm (n=6); carpus 6.9-8.5 times as long as wide (n=35), 1.4-1.9 times as long as merus (n=5).

Third pereopod (Fig. 5F,I) slender, dactylus 3.8-5.3 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 2 accessory spines on flexor margin; propodus 14.7-24.2 times as long as wide, 4.9-6.2 times as long as dactylus; carpus 7.5-9.2 times as long as wide, 0.6-0.7 times as long as propodus, 0.5-0.6 times as long as merus; merus 11.0-12.4 times as long as wide, bearing 3-4 strong, movable spines on posterior margin of outer surface.

Fifth pereopod slender (Fig. 5G,J), dactylus 3.0-5.1 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 25-30 accessory spines on flexor margin; propodus 17.3-24.2 times as long as wide, 4.4-7.0 times as long as dactylus; carpus 6.6-9.0 times as long as wide, 0.5 times as long as propodus, 0.6 times as long as merus; merus 9.4-13.8 times as long as wide, bearing 1-3 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 5K) elongated triangular, 1.7-2.3 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 5L) 0.8-0.9 times length of appendix masculina (n=5).

Ovigerous females with 8-14 eggs (n=7 females); egg size 1.0-1.2 x 0.5-0.7 mm (n=88, eggs with and without eyes).

**Distribution.** – *C. dennerli* is endemic to Lake Matano and widely distributed within the lake (Fig. 4A).

**Biology and ecology.** – *C. dennerli* is a hard substrate dweller (rocks) occurring in different water depths (from shallow water to approx. –10 m), on or under small rocks, and between boulders. When disturbed, it tries to escape side- or downwards rather than in other directions, but frequently stays attached to a rock when it is uplifted.

**Colour pattern.** – *C. dennerli* has one of the most conspicuous colour patterns among the ancient lake species (Fig. 4B-C). Body and most appendages are primarily dark red to purple; body covered with several white conspicuous spots and one distinct white dot on the dorsodistal part of the abdomen. Chela and carpus of the first and second pereopod bright white and distinctly contrasting the otherwise red colour. Antenna, antenulla, and scaphocerite also white. When feeding, the white chelipeds were observed to be always clearly visible, whereas the rest of the (dark coloured) body was more or less camouflaged; eggs are also dark red. Under stress, red body colour can change to blue, but only temporarily. This change of colour was only observed in a small water tank minutes after being caught.

**Etymology.** – *Caridina dennerli*, new species, is dedicated to the German company Dennerle GmbH, which kindly supported the authors' shrimp project on the ancient lake species of Sulawesi.

**Taxonomic remarks.** – The slightly falciform rostrum is a more constant character in *C. dennerli* than in other species. Thus, it is already distinguishable in most cases at first sight. With regard to the rostrum, *C. dennerli* mainly resembles *C. holthuisi*, but also other species from Lake Towuti, e.g. the broad rostrum morph of *C. striata*, although it is more slender than in *C. holthuisi* and usually broader and shorter than in *C. striata* (reaching near or to end of scaphocerite vs. longer



than in *C. striata*). It differs from *C. holthuisi* not only in its substrate preference (rocks vs. leaf litter in *C. holthuisi*) and colour pattern (compare respective description), but also by a different number of ventral teeth on the rostrum (5-11, median 9 vs. 3-7, median 5 in *C. holthuisi*) and distinctly more slender pereopods in *C. dennerli* (for example chela of first pereopod 2.4-3.8, median 2.7 vs. 1.8-2.3, median 2.1 in *C. holthuisi*).

In the molecular phylogeny (Figs. 63-64), *C. dennerli* is genetically distinct from the other species mentioned above.

***Caridina glaubrechtii*, new species**  
(Figs. 7-9; Table 4)

*Caridina* sp.1 – von Rintelen et al., 2007b: 262, fig. 2b.

**Material examined.** – Holotype: female (cl 2.7 mm)(MZB Cru 2122), Lake Towuti, west shore, south of Cape Timbalo, 02°42.91'S, 121°26.78'E, loc. 94-03, coll. K. & T. von Rintelen, 4 Oct.2003.

Paratypes (all Lake Towuti) – 5 ex. (ZMB 29053, some SEM material), south shore, approx. 2 km east of Cape Mea, 02°55.8'S, 121°26.92'E, loc. 74-03, coll. K. & T. von Rintelen, 28 Sep.2003; 2 ex. (ZMB 29074, some SEM material), north shore, bay east of

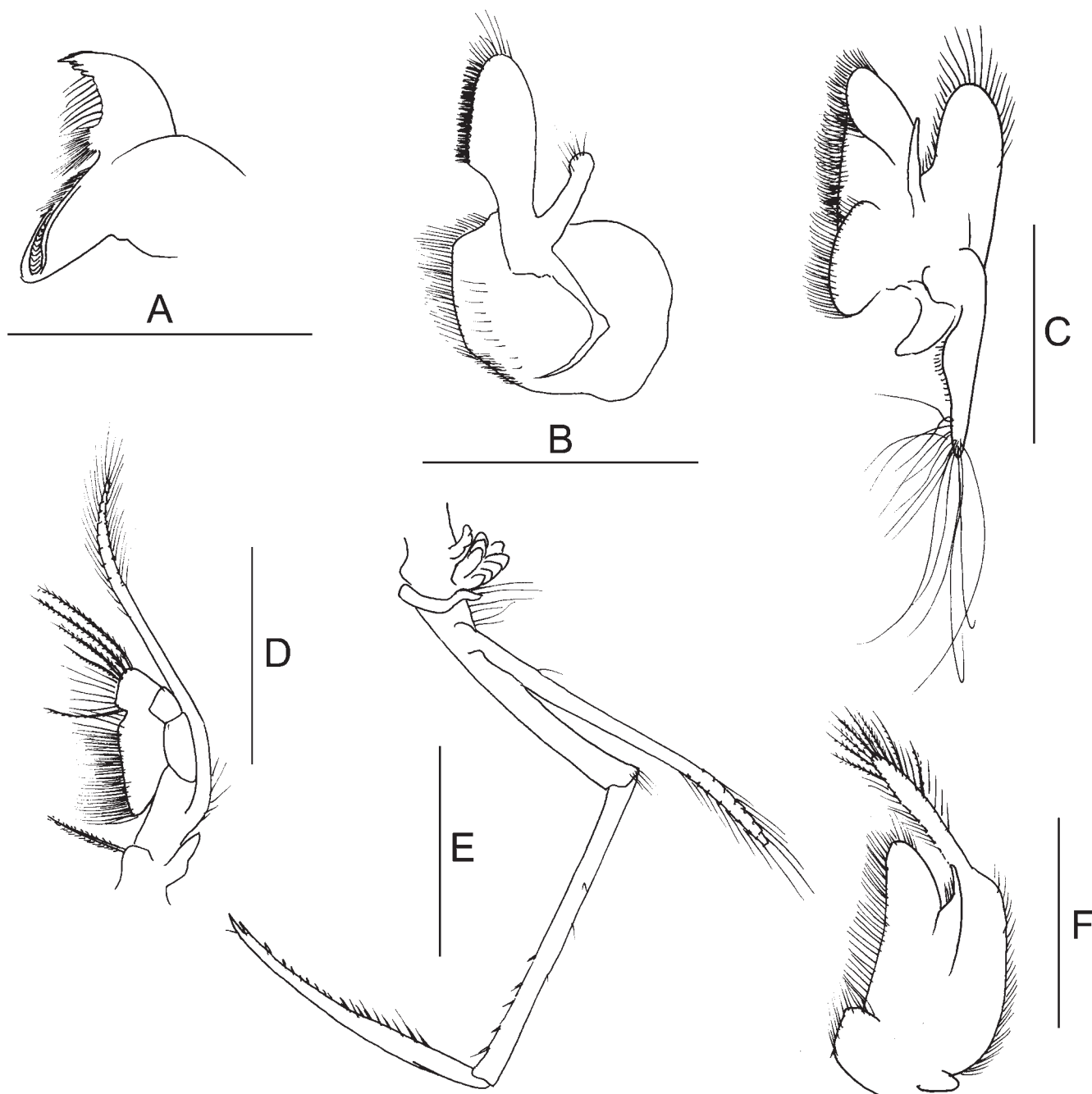


Fig. 6. *Caridina dennerli* from the Malili lake system. A. Mandible (ZMB 29024); B. Maxillula; C. Maxilla; D. second maxilliped; E. third maxilliped; F. first maxilliped. Scale bars: A-F = 1mm.

Cape Bintu, 02°39.48'S, 121°33.25'E, loc. 68-03, coll. K. & T. von Rintelen, 26 Sep.2003; 26 ex. (MZB Cru 1825, n=11; ZMB 29077, n=15), west shore, south of Cape Timbalo, 02°42.91'S, 121°26.78'E, loc. 94-03, coll. K. & T. von Rintelen, 4 Oct.2003; 1 ex. (ZMB 29086, some SEM material), Larona River, 02°45.06'S, 121°20.12'E, loc. 50-03, coll. K. & T. von Rintelen, 21 Sep.2003; 12 ex. (MZB Cru 1826, n=6; ZMB 29109, n=6), west shore, north of Cape Wasupute, 02°46.9'S, 121°27.94'E, loc. 78-03, coll. K. & T. von Rintelen, 26 Jul.2004; 7 ex. (ZMB 29301), west shore, west of Cape Timbalo, 02°42.631'S, 121°26.389'E, loc. 145-04, coll. K. & T. von Rintelen, 26 Jul.2004; 3 ex. (ZMB 29335), northwest shore, 02°40.897'S, 121°25.015'E, loc. 143-04, coll. K. & T. von Rintelen, 25 Jul.2004; 2 ex. (MZB Cru 1827), west shore, Cape Bakara, 02°40.771'S, 121°26.11'E, loc. 144-04, on rocks in deeper water, coll. K. & T. von Rintelen, 26 Jul.2004.

**Description.** – Carapace length 2.3-3.4 mm (n=11). Rostrum (Fig. 8A; Table 4) long, reaching beyond end of scaphocerite, 0.9-1.7 times as long as carapace (n=12), armed dorsally with 11-17 teeth (including 2-5 teeth posterior to orbital margin), anterior less densely spaced, armed ventrally with 5-16 teeth (n=9). Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes

well developed, anterior end 0.6-0.8 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 1.0 times as long as carapace (n=5), second segment 1.8-2.1 times length of third segment, third segment 0.3 times length of basal segment. Stylocerite reaching 0.9 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 8D) 4.0-5.7 times as long as wide (n=5).

Sixth abdominal somite 0.5-0.8 times length of carapace (n=10), 1.6-2.0 times as long as fifth somite (n=5), 0.8-1.2 times length of telson (n=11). Telson (Fig. 8F-G,M-N) 3.2-3.4 times as long as wide (n=5), distal margin rounded, without projection, with 3-4 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 3-4 pairs of spines, lateral pair distinctly longer than intermediate spines, median pair or median spine shortest. Preanal carina (Fig. 8B) rounded, without a spine. Uropodal diaeresis (Fig. 8C) with 11-14 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair

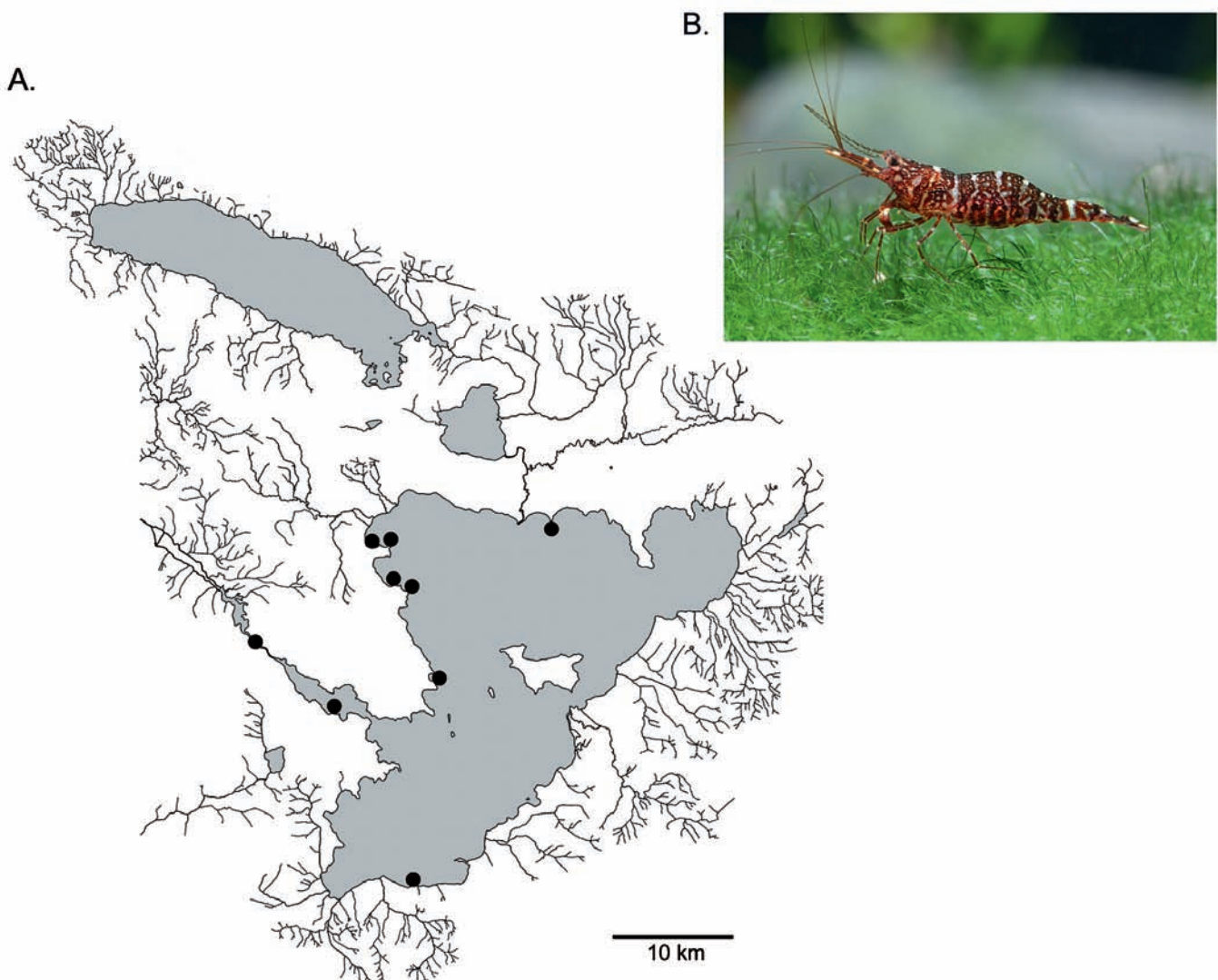


Fig. 7. *Caridina glaubrechti* from the Malili lake system. A. Distribution. B. Colour pattern of living animal (not to scale). Picture courtesy of Chris Lukhaup.

Table 4. Summary of standard morphometric parameters for *Caridina glaubrechtii*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	2.3-3.4	2.9 $\pm$ 0.3	2.9	11
rl / cl	0.9-1.7	1.2 $\pm$ 0.3	1.1	12
n dorsal rostral teeth	11-17	15 $\pm$ 2	15	9
n ventral rostral teeth	5-16	9 $\pm$ 4	8	9
abds6 / cl	0.5-0.8	0.7 $\pm$ 0.1	0.7	10
abds6 / abds5	1.6-2.0	1.8 $\pm$ 0.2	1.8	5
abds6 / h tel	0.8-1.2	1.0 $\pm$ 0.1	1.0	11
h tel / w tel	3.2-3.4	3.3 $\pm$ 0.1	3.3	5
n spines uropodal diaeresis	11-14	13 $\pm$ 1	12	5
h ch1 / w ch1	2.0-2.4	2.2 $\pm$ 0.2	2.2	8
h ch1 / h ca1	1.1-1.4	1.2 $\pm$ 0.1	1.2	12
h ca1 / w ca1	1.9-3.4	2.6 $\pm$ 0.5	2.6	8
h ch2 / w ch2	2.3-3.2	2.8 $\pm$ 0.3	2.9	8
h ch2 / h ca2	0.7-0.8	0.8 $\pm$ 0.0	0.8	11
h ca2 / w ca2	4.8-6.7	5.7 $\pm$ 0.7	5.7	8
n spines p3	2-5	4 $\pm$ 1	4	4
n spines p5	14-35	26 $\pm$ 9	28	4

of podobranchs on second maxilliped reduced strongly to a laminate form. Epipod reduced or totally absent from the first pereopod. Incisor process of mandible (Fig. 9A) ending in a row of 4-5 small teeth, molar process truncated. Lower lacinia of maxillula (Fig. 9B) broadly rounded, upper lacinia elongate, with numerous distinct teeth and setae on inner margin, palp slender. Upper endites of maxilla (Fig. 9C) subdivided, palp short, scaphognathite tapering posteriorly with numerous long, curved setae at posterior end. Distal end of palp of first maxilliped (Fig. 9F) triangular, not ending with a finger-like projection; flagellum of the exopod very elongated, endopod high, not exceeding the flagellum of exopod in length. Second maxilliped (Fig. 9D) typical. Third maxilliped (Fig. 9E) with ultimate segment as long as penultimate segment.

Chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig. 8O-Q); chela of first pereopod 2.0-2.4 times as long as wide (n=8), 1.1-1.4 times length of carpus (n=12); tips of fingers rounded, without hooks; dactylus 1.1-1.3 times as long as palm (n=5); carpus 1.9-3.4 times as long as wide (n=8), 1.1-1.4 times length of merus (n=5). Chela of second pereopod 2.3-3.2 times as long as wide (n=8), 0.7-0.8 times length of carpus (n=11); tips of fingers rounded, without hooks, dactylus 1.2-1.5 times as long as palm (n=5); carpus 4.8-6.7 times as long as wide (n=8), 1.4 times as long as merus (n=5).

Third pereopod (Fig. 8H,E) slender, dactylus 3.6-4.2 times as long as wide (terminal spine included, without spines of flexor margin; n=4), terminating in one large claw with 2-5 accessory spines on flexor margin; propodus 11.4-15.0 times as long as wide, 4.2-5.5 times as long as dactylus; carpus 5.8-7.5 times as long as wide, 0.6-0.7 times as long as propodus, 0.5 times as long as merus; merus 9.0-11.3

times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Fifth pereopod slender (Fig. 8I-J), dactylus 3.8-4.5 times as long as wide (terminal spine included, without spines of flexor margin; n=4), terminating in one large claw with 14-35 accessory spines on flexor margin; propodus 14.0-21.8 times as long as wide, 4.1-6.5 times as long as dactylus; carpus 5.0-7.2 times as long as wide, 0.5-0.6 times as long as propodus, 0.6-0.7 times as long as merus; merus 8.5-12.0 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 8K) elongated triangular, 1.8-2.7 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 39L) 0.8-0.9 times length of appendix masculina (n=5).

Ovigerous females with 20 eggs (n=2 females); egg size 0.8-1.0 x 0.5-0.6 mm (n=40, eggs with and without eyes).

**Distribution.** – *C. glaubrechtii* is endemic to Lake Towuti and was mainly found in the western part of the lake (Fig. 7A).

**Biology and ecology.** – *C. glaubrechtii* is a hard substrate dweller on rocks and was mainly found in shallow water regions on smaller rocks, but also in deeper water zones (below 3 m) on larger rocks (boulders). When disturbed, it tries to escape side- or downwards rather than in other directions. This is a behaviour also typical for other rock dwellers (KvR, pers. observ.). *C. glaubrechtii* is often found in syntopy with other rock dwellers in Lake Towuti, such as *C. profundicola* and *C. spinata*, but particularly *C. striata* and *C. woltereckae*.

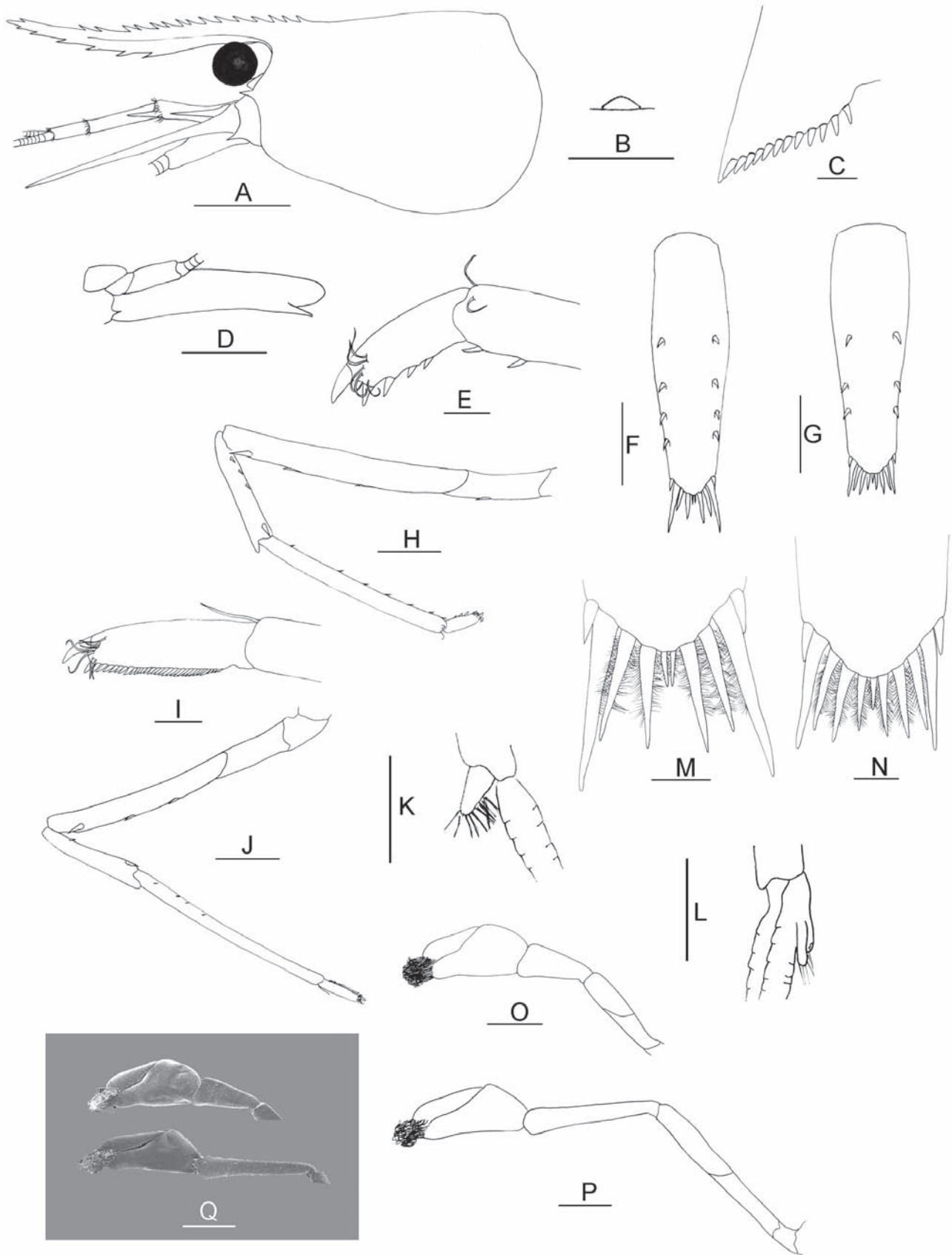


Fig. 8. *Caridina glaubrechti* from the Malili lake system. A. Cephalothorax and cephalic appendages, female (ZMB 29053); B. Preanal carina, male (ZMB 29109); C. Uropodal diaeresis, female (ZMB 29053); D. Scaphocerite, male (ZMB 29109); E. Dactylus of third pereiopod, female (ZMB 29074); F. Telson, female (ZMB 29053); G. Telson, another female (ZMB 29053); H. Third pereiopod, female (ZMB 29074); I. Dactylus of fifth pereiopod; J. Fifth pereiopod; K. Endopod of male first pleopod (ZMB 29109); L. Appendix masculina of male second pleopod; M. Distal end of telson, female (ZMB 29053); N. Distal end of telson, another female (ZMB 29053); O. First pereiopod, female (ZMB 29053); P. Second pereiopod; Q. SEM image of chela and carpus of first and second pereiopods, female (ZMB 29053). Scale bars: A, D = 1.0 mm; B, F-H, J-L, O-Q = 0.5 mm; C, E, I, M-N = 0.1 mm.

**Colour pattern.** – The primary colour of *C. glaubrechtii* is brown with several white bands or patches all over the body (including pereopods and uropods; Fig. 7B). A conspicuous white band is visible at the distal part of the abdomen. Appendages are transparent or partly brownish. Eggs are brown. This colour pattern remains visible even if the shrimp is under stress; the intensity of the colour merely fades.

**Etymology.** – *Caridina glaubrechtii*, new species, is dedicated to Matthias Glaubrecht, who initiated the current research on endemic species flocks from the ancient lakes of Sulawesi, and who also collected several shrimp specimens.

**Taxonomic remarks.** – The colour pattern of *C. glaubrechtii* closely resembles the colour pattern of *C. tenuirostris*, but

both species not only differ in their substrate preference (rocks vs. wood in *C. tenuirostris*), but by the continuous dorsal denticulation of the rostrum (vs. anterior dorsal part always completely unarmed in *C. tenuirostris*), a different number of spines on the uropodal diaeresis (11-14, median 12 vs. 7-8, median 8 in *C. tenuirostris*), and on the dactylus of the fifth pereopod (14-35, median 28 vs. 11-15, median 14 in *C. tenuirostris*).

As alcohol bleached material, *C. glaubrechtii* is almost identical with *C. striata* and *C. woltereckae*, although the colour pattern in living specimens always allows an unambiguous separation. It slightly differs from *C. woltereckae* by a higher number of spines on the dactylus of the fifth pereopod (14-35, median 28 vs. 13-22, median 20 in

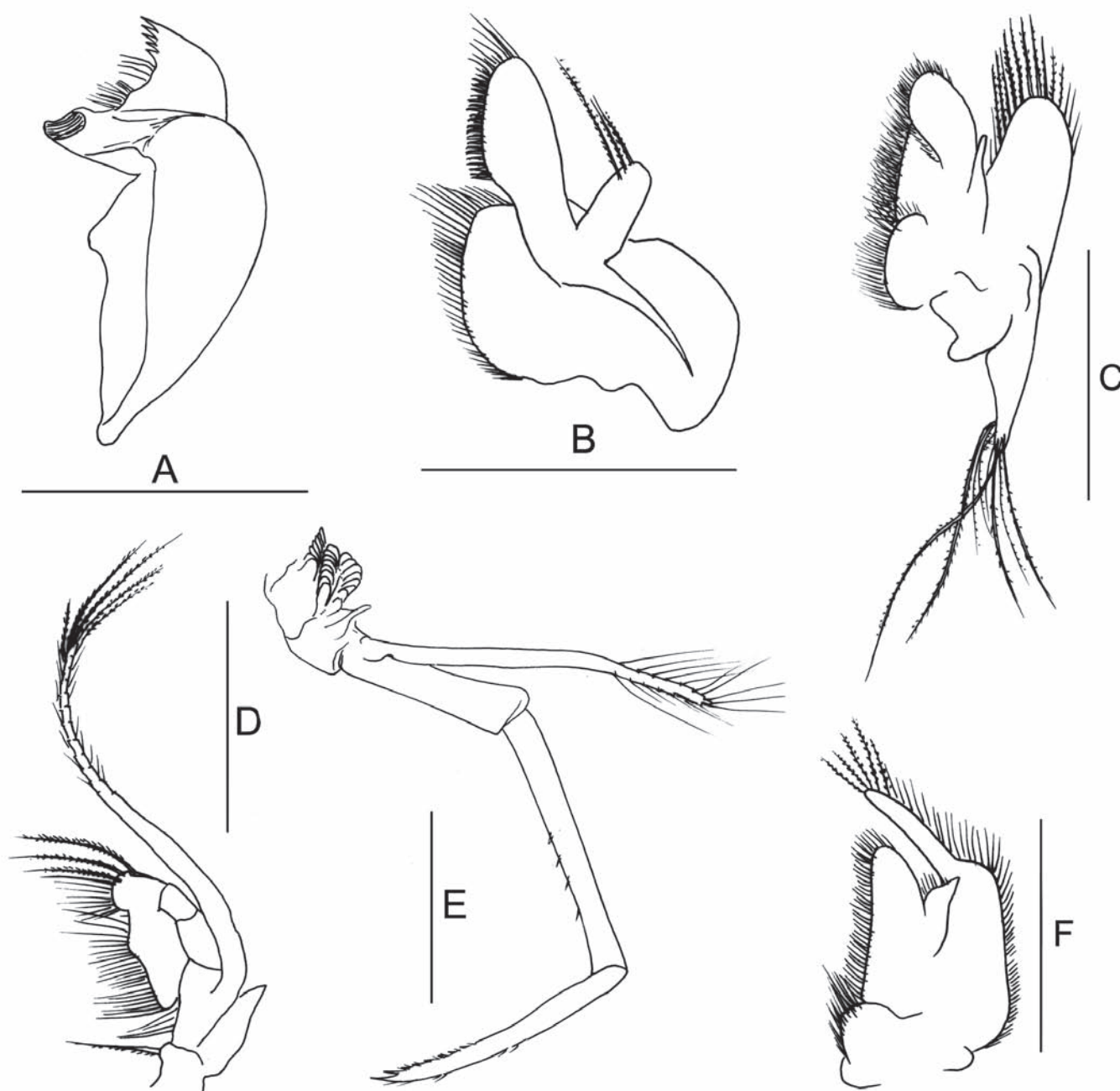


Fig. 9. *Caridina glaubrechtii* from the Malili lake system. A. Mandible (ZMB 29053); B. Maxillula; C. Maxilla; D. second maxilliped; E. third maxilliped; F. first maxilliped. Scale bars: A-F = 1mm.

*C. woltereckae*). Also, the dimorphic character of the rostrum in *C. striata* could not be observed in *C. glaubrechtii*.

In the molecular phylogeny (Figs. 63-64), *C. glaubrechtii* forms a single clade with the other rock dwellers *C. striata* and *C. woltereckae*, and the sponge dweller *C. spongicola*, but their relationship is not resolved within this clade (compare von Rintelen et al., 2007b; for further details see taxonomic remarks on *C. striata*).

***Caridina holthuisi*, new species**  
(Figs. 10-12, Table 5)

*Caridina opaensis* – Woltereck, 1937a: 222, fig. I.4, pls. 3,6 (locality: Matanno [Matano], Soroako).

*Cardina opaensis* – Brooks, 1950: 168 (erroneous spelling).

**Material examined.** – Holotype – ovigerous female (cl 3.2 mm)(MZB Cru 2125), Lake Matano, south shore, canal between island and mainland, 02°28.46'S, 121°15.83'E, loc. 62-03, on leaf litter, coll. K. & T. von Rintelen, 1 Oct.2003.

Paratypes (Lake Matano) – 7 ex. (ZMB 29272), south shore, 02°27.85'S, 121°13.87'E, loc. 125-04, on leaf litter, coll. K. & T. von Rintelen, 1 Aug.2004; 5 ex. (ZMB 29065, some SEM material), south shore, 02°27.84'S, 121°13.88'E, loc. 63-03, on leaf litter, coll. K. & T. von Rintelen, 24 Sep.2003; 4 ex. (ZMB 29073), south shore, at small islands, 02°28.461'S, 121°15.591'E, loc. 137-04, on macrophytes, coll. K. & T. von Rintelen, 24 Jul.2004; 44 ex. (MZB Cru 1790, n=22; ZMB 29075, n=22, some SEM material), south shore, canal between island and mainland, 02°28.46'S, 121°15.83'E, loc. 62-03, on leaf litter, coll. K. & T. von Rintelen, 1 Oct.2003; 24 ex. (MZB Cru 1791, n=11; ZMB 29105, n=13, some SEM material), north shore, 02°26.36'S, 121°19.03'E, loc. 84-03, on leaf litter, coll. K. & T. von Rintelen, 1 Oct.2003; 6 ex. (ZMB 29107, some SEM material), south shore, Soroako, Salonsa, Pantai Ide, 02°30.89'S, 121°20.53'E, loc. 40-03, on mixed substrate, coll. K. & T. von Rintelen, 17 Sep.2003; 1 ex. (ZMB 29139), north shore, 02°29.75'S, 121°25.81'E, loc. 42-03, on rocks, coll. K. & T. von Rintelen, 17 Sept. 2003; 4 ex. (ZMB 29140), south shore, 02°28.5'S, 121°15.55'E, loc. 139-04, on mixed substrate, coll. K. & T. von Rintelen, 24 Jul.2004; 16 ex. (MZB Cru 1792, n=8; ZMB 29189, n=8), at small islands, 02°28.458'S, 121°15.57'E, loc. F4-02, on mixed substrate, coll. F. Herder, 2 Nov.2002; 1 ex. (ZMB 29225), north shore, 02°27.28'S, 121°21.21'E, loc. 98-03, on leaf litter, coll. K. & T. von Rintelen, 5 Oct.2003; 4 ex. (ZMB 29227), south shore, 02°27.84'S, 121°13.88'E, loc. 01-05, on macrophytes, coll. K. & T. von Rintelen, 1 Jan.2005; 1 ex. (ZMB 29231), south shore, Soroako, Salonsa, INCO boat house, 02°30.71'S, 121°20.45'E, loc. 19-03, on rocks, coll. K. & T. von Rintelen, 19 Sep.2003; 6 ex. (ZMB 29232, n=6 and some juveniles), north shore, 02°28.42'S, 121°24.21'E, loc. 41-03, on leaf litter, coll. K. & T. von Rintelen, 17 Sep.2003; 9 ex. (MZB Cru 1793, n=4; ZMB 29286, n=5, some SEM material), northwest shore, 02°25.742'S, 121°13.797'E, loc. 134-04, on leaf litter, coll. K. & T. von Rintelen, 23 Jul.2004; 11 ex. (MZB Cru 1794, n=5; ZMB 29185, n=6), Matano catchment, river, near mouth at northwest corner of Lake Matano, 02°25.88'S, 121°13.08'E, loc. 24-03, on leaf litter, coll. K. & T. von Rintelen, 13 Sep.2003.

Paratypes (Lake Mahalona) –12 ex. (MZB Cru 1795, n=6; ZMB 29059, n=6), Lake Mahalona (no further details given), loc. F3-02, substrate unknown, coll. J. Frommen, 1 Nov.2002; 9 ex. (ZMB 29063, n=9 and some juveniles, some SEM material), east shore,

at mouth of Petea River, 02°34.54'S, 121°30.48'E, loc. 55-03, on leaf litter, coll. K. & T. von Rintelen, 23 Sep.2003; 11 ex. (MZB Cru 1796, n=5; ZMB 29324, n=6), east shore, estuary of Ponsoa River, 02°35.101'S, 121°30.681'E, loc. 146-04, on *Ottelia*, coll. P. Koller, K. & T. von Rintelen, 3 Aug.2004.

Paratypes (Lake Towuti) – 33 ex. (MZB Cru 1797, n=15; ZMB 29036, n=18), southwest shore, west of Cape Tetetu, 02°54.13'S, 121°23.78'E, loc. 76-03, on leaf litter, coll. K. & T. von Rintelen, 28 Sep.2003; 3 ex. (ZMB 29078, some SEM material), west shore, at entrance to outlet bay, Cape Larona, 02°48.43'S, 121°24.75'E, loc. 73-03, on leaf litter, coll. K. & T. von Rintelen, 27 Sep.2003; 21 ex. (MZB Cru 1798, n=11; ZMB 29228, n=10 and some juveniles), east shore, 02°40.84'S, 121°41.32'E, loc. 87-03, on leaf litter, coll. K. & T. von Rintelen, 2 Oct.2003; 4 ex. (ZMB 29303, some SEM material), northeast shore, at Lengkona, 02°40.483'S, 121°41.382'E, loc. 116-04, on leaf litter, coll. K. & T. von Rintelen, 28 Jul.2004; 3 ex. (MZB Cru 1799), west shore, west of Cape Timballo, 02°42.631'S, 121°26.389'E, loc. 145-04, on mixed substrate, coll. K. & T. von Rintelen, 26 Jul.2004; 2 ex. (MZB Cru 1800), northwest shore, south of Timampu, 02°39.466'S, 121°25.859'E, loc. 140-04, on macrophytes, coll. K. & T. von Rintelen, 25 Jul.2004.

**Comparative material examined.** – *Caridina opaensis* Roux, 1904: 547, pl. 9, Figs. 8-10 (type locality: Southeast Sulawesi, Lake Opa, 30 m above sealevel).

Syntypes – 2 females (cl 2.9-3.3 mm) (NHMB 9a), Southeast Sulawesi, Opa, Sulawesi, Indonesia, coll. Sarasin, 1904.

Others (all Southeast Sulawesi): 1 ex. (ZMB 29008), Benua River, northern arm, 04°13.388'S, 122°6.397'E, loc. 85-05, coll. M. Glaubrecht, K. & T. von Rintelen, 31 May 2005; 1 ex. (ZMB 29010), stream at road Kendari – Lapuko, near Mulyasari, 04°7.34'S, 122°36.82'E, loc. 103-05, coll. K. & T. von Rintelen, 1 Jun.2005; 1 ex. (ZMB 29018), stream at Labeala, east of Pundihaha, road Kendari – Kolaka, 03°57.987'S, 122°20.739'E, loc. 77-05, coll. M. Glaubrecht, K. & T. von Rintelen, 30 May 2005; 1 ex. (ZMB 29338), stream in Pruijala, north of Aopa area, 04°3.67'S, 122°6.845'E, loc. 83-05, coll. M. Glaubrecht, K. & T. von Rintelen, 31 May 2005; 1 ex. (ZMB 29339), Simbune River, approx. 1 km northeast of Raterate, road Kendari – Kolaka, 04°2.326'S, 121°54.204'E, loc. 79-05, coll. M. Glaubrecht, K. & T. von Rintelen, 30 May 2005; 1 ex. (ZMB 29340), Humbuti River, northwest of Abuki, 03°38.91'S, 121°52.38'E, loc. 78-05, coll. M. Glaubrecht, K. & T. von Rintelen, 30 May 2005.

**Description.** – Carapace length 2.3-3.8 mm (n=29). Rostrum (Fig. 11A-E; Table 5) usually broad, reaching near or slightly beyond end of scaphocerite, 0.6-1.2 times as long as carapace (n=32), armed dorsally with 14-28 teeth (including 4-8 teeth posterior to orbital margin), armed ventrally with 3-7 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.5-0.6 times length of basal segment of antennular peduncle (n=6). Antennular peduncle 0.8-1.0 times as long as carapace (n=6), second segment 1.6-2.1 times length of third segment, third segment 0.3-0.4 times length of basal segment. Stylocerite reaching 0.9-1.0 times length of basal segment of antennular peduncle (n=6). Scaphocerite (Fig. 11H) 3.8-4.8 times as long as wide (n=5).

Sixth abdominal somite 0.5-0.7 times length of carapace (n=15), 1.4-1.8 times as long as fifth somite (n=15), 0.9-1.0

times length of telson (n=10). Telson (Fig. 11J-K) 2.9-3.5 times as long as wide (n=6), distal margin rounded, without projection, with 3-4 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 3-4 pairs of spines, lateral pair longer than intermediate pairs, median pair shortest. Preanal carina (Fig. 11I) with a spine. Uropodal diaeresis (Fig. 11L) with 12-13 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipod present on first two pereopods.

Incisor process of mandible (Fig. 12A) ending in a row of 3-4 small teeth, molar process truncated. Lower lacinia of maxillula (Fig. 12B) broadly rounded, upper lacinia elongate, with numerous distinct teeth and setae on inner margin, palp slender. Upper endites of maxilla (Fig. 12C) subdivided, palp short, scaphognathite tapering posteriorly with numerous long, curved setae at posterior end. Distal end of palp of first maxilliped (Fig. 12F) triangular, with a finger-like projection; flagellum of the exopod very elongated, endopod high, not exceeding the flagellum of exopod in length. Second maxilliped (Fig. 12E) typical. Third maxilliped (Fig. 12D) with ultimate segment distinctly shorter than penultimate segment.

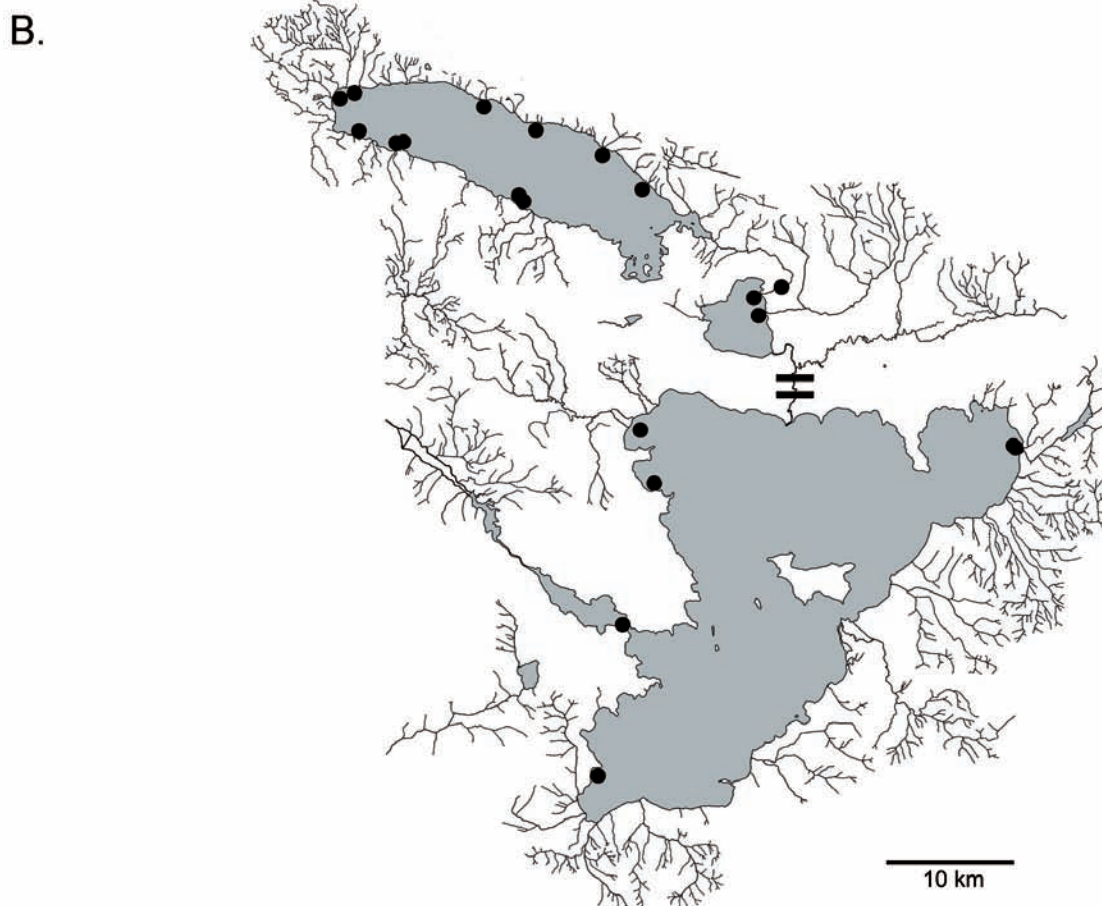


Fig. 10. *Caridina holthuisi* from the Malili lake system. A. Distribution (the equal sign roughly marks the geographic boundary between the two genetic clades; compare taxonomic remarks). B. Colour pattern of living animal (not to scale). Pictures courtesy of Chris Lukhaup.

Table 5. Summary of standard morphometric parameters for *Caridina holthuisi*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	2.3-3.8	2.8 $\pm$ 0.4	2.7	29
rl / cl	0.6-1.2	0.9 $\pm$ 0.1	0.9	32
n dorsal rostral teeth	14-28	20 $\pm$ 3	20	32
n ventral rostral teeth	3-7	5 $\pm$ 1	5	32
abds6 / cl	0.5-0.7	0.6 $\pm$ 0.1	0.6	15
abds6 / abds5	1.4-1.8	1.6 $\pm$ 0.1	1.6	15
abds6 / h tel	0.9-1.0	0.9 $\pm$ 0.0	0.9	10
h tel / w tel	2.9-3.5	3.3 $\pm$ 0.2	3.4	6
n spines uropodal diaeresis	12-13	13 $\pm$ 1	13	5
h ch1 / w ch1	1.8-2.3	2.1 $\pm$ 0.2	2.1	18
h ch1 / h ca1	1.1-1.4	1.2 $\pm$ 0.1	1.2	17
h ca1 / w ca1	2.0-3.1	2.7 $\pm$ 0.3	2.7	13
h ch2 / w ch2	2.3-3.5	2.8 $\pm$ 0.3	2.8	18
h ch2 / h ca2	0.7-0.9	0.8 $\pm$ 0.1	0.7	22
h ca2 / w ca2	4.3-7.0	5.7 $\pm$ 0.9	5.7	18
n spines p3	3-6	4 $\pm$ 1	4	5
n spines p5	27-39	34 $\pm$ 5	33	5

Chela and carpus of first pereiopod distinctly stouter and broader than chela and carpus of second pereiopod (Fig. 11S-T); chela of first pereiopod 1.8-2.3 times as long as wide (n=18), 1.1-1.4 times length of carpus (n=17); tips of fingers rounded, without hooks; dactylus 0.9-1.3 times as long as palm (n=9); carpus 2.0-3.1 times as long as wide (n=13), 1.1-1.3 times length of merus (n=9). Chela of second pereiopod 2.3-3.5 times as long as wide (n=18), 0.7-0.9 times length of carpus (n=22); tips of fingers rounded, without hooks, dactylus 1.0-1.4 times as long as palm (n=9); carpus 4.3-7.0 times as long as wide (n=18), 1.2-1.5 times as long as merus (n=10).

Third pereiopod (Fig. 11M,O) slender, dactylus 4.2-5.0 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 3-6 accessory spines on flexor margin; propodus 8.8-13.5 times as long as wide, 2.8-3.8 times as long as dactylus; carpus 4.8-5.6 times as long as wide, 0.6-0.7 times as long as propodus, 0.5-0.6 times as long as merus; merus 7.2-8.8 times as long as wide, bearing 3-4 strong, movable spines on posterior margin of outer surface.

Fifth pereiopod slender (Fig. 11N,P), dactylus 3.7-6.3 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 27-39 accessory spines on flexor margin; propodus 11.0-15.0 times as long as wide, 2.7-3.1 times as long as dactylus; carpus 4.6-5.5 times as long as wide, 0.5 times as long as propodus, 0.6-0.7 times as long as merus; merus 6.5-8.5 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 11Q) elongated triangular, 1.8-2.5 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second

pleopod (Fig. 11R) 0.8-0.9 times length of appendix masculina (n=5).

Ovigerous females with 19-25 eggs (n=2 females); egg size 0.8-1.0 x 0.5-0.6 mm (n=38, eggs with and without eyes).

**Distribution.** – Endemic to the Malili lake system; occurring in all three major lakes and in Petea River, widely distributed within each lake (Fig. 10B).

**Biology and ecology.** – *C. holthuisi* is a soft substrate dweller, mainly found under dead leaves (leaf litter), but also sporadically on macrophytes. Its colour pattern is similar to its substrate, the usually dark brown leaves that can be found covering the shallow bottom in various shore areas. When disturbed, *C. holthuisi* rather tries to escape downwards than in other directions to hide under its substrate. When a pile of dead leaves is sampled with a dip net, specimens usually accumulate at the bottom of the net.

**Colour pattern.** – The body, and often also the appendages too, show a vivid dark brown colour similarly to the brown colour of the species' leaf substrate (Fig. 10A). Various white-beige markings (usually transversal stripes or a dorsal longitudinal stripe) are possible. Eggs are also dark brown.

**Etymology.** – *Caridina holthuisi*, new species, is named in honour of L.B. Holthuis as one of the well-known carcinologist of our time, who also contributed greatly to our knowledge of the shrimp genus *Caridina*.

**Taxonomic remarks.** – Woltereck (1937a, b) described some specimens from Lake Matano as *Caridina opaensis* Roux, 1904, and thus mentioned it as the only non-endemic species in the Malili lake system. Brooks (1950: 169) even



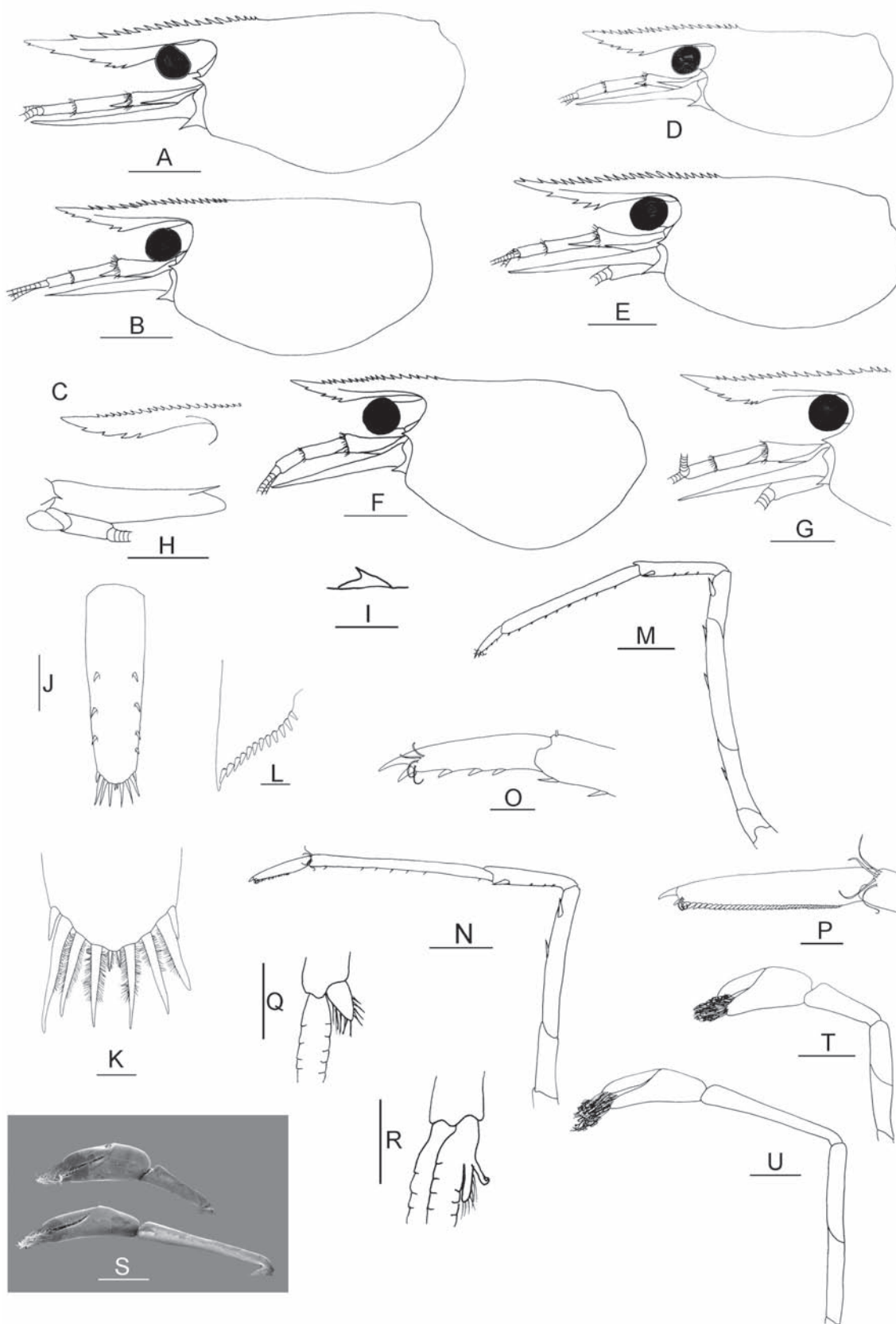


Fig. 11. *Caridina holthuisi* from the Malili lake system and *C. opaensis* from SE Sulawesi. Cephalothorax and cephalic appendages from: A. Female, MT (ZMB 29286); B. Male, MT (ZMB 29286); C. Woltereck's drawing of the rostrum (modified from 1937a); D. Female, MT (ZMB 29107); E. Female, TW (ZMB 29303); F. Female, SE Sul (ZMB 29338); G. Female, SE Sul (ZMB 29339). H. Scaphocerite, male, MT (ZMB 29232); I. Preanal carina; J. Telson, female, MT (ZMB 29105); K. Distal end of telson; L. Uropodal diaeresis; M. Third pereiopod, female MT (ZMB 29075); N. Fifth pereiopod; O. Dactylus of third pereiopod; P. Dactylus of fifth pereiopod; Q. Endopod of male first pleopod, MT (ZMB 29232); R. Appendix masculina of male second pleopod; S. SEM image of chela and carpus of first and second pereiopods, female, MT (ZMB 29286); T. First pereiopod, female (ZMB 29075); U. Second pereiopod. Scale bars: A-B, D-H = 1.0 mm; I-J, M-N, Q-U = 0.5 mm; K-L, O-P = 0.1 mm; C = no scale available.

discussed the origin of Lake Matano's fauna based on the presumed non-endemism of this species. However, albeit some first glance similarities between the true *C. opaensis* Roux, 1904 from Southeast Sulawesi and Woltereck's *C. opaensis*, i.e. *C. holthuisi*, new species (Fig. 29F-G), both are morphologically distinct species and Woltereck's '*C. opaensis*' is here considered as to be *C. holthuisi*, new species. *C. holthuisi* can be distinguished from *C. opaensis* by its generally smaller size (cl 2.3-3.8, mean 2.8 vs. 2.9-4.9, mean 4.0, n=23 in *C. opaensis*), a generally longer rostrum compared to the carapace length (0.6-1.2, mean 0.9, vs. 0.40-0.8, mean 0.7, n=25 in *C. opaensis*), a lower number of movable spinules on the uropodal diaeresis (12-13 vs. 14-19,

n=6, in *C. opaensis*), and a lower number of accessory spines on flexor margin of dactylus of the third and fifth pereopod (3-6 and 31-39 vs. 6 and 54-64, n=3 in *C. opaensis*).

*C. holthuisi* slightly resembles *C. dennerli*, but differs not only in its substrate preference (leaf litter vs. rocks in *C. dennerli*), or colour pattern (compare respective description), but also by a broader rostrum, a different number of ventral teeth on the rostrum (5-11, median 9 vs. 3-7, median 5), and distinctly stouter pereopods in *C. holthuisi* (for example chela of first pereopod 1.8-2.3, median 2.1 vs. 2.4-3.8, median 2.7 in *C. dennerli*).

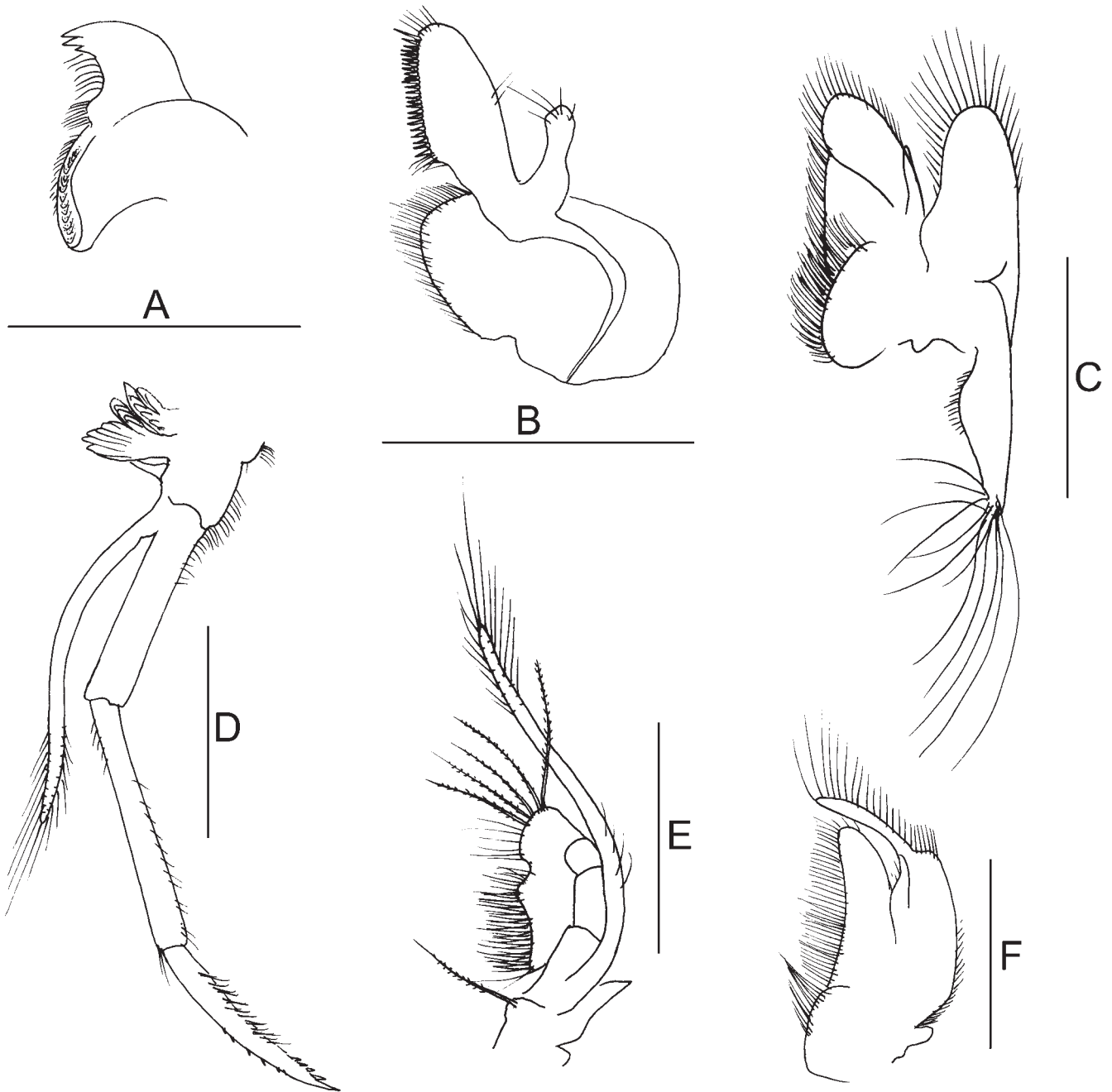


Fig. 12. *Caridina holthuisi* from the Malili lake system. A. Mandible (ZMB 29286); B. Maxillula; C. Maxilla; D. third maxilliped; E. second maxilliped; F. first maxilliped. Scale bars: A-F = 1mm.

*C. holthuisi* can resemble *C. masapi*, but the rostrum in *C. masapi* usually differs by a more or less dense denticulation on the dorsal margin, and a straighter and broader shape (vs. usually with a conspicuous unarmed gap on the dorsal margin and a more slender and cambered shape in *C. masapi*).

Besides the morphological differences, *C. holthuisi* is genetically distinct from *C. opaensis* (Fig. 63). All sequenced specimens of *C. opaensis* from and around the type locality are not closely related to any of the ancient lake species (compare von Rintelen et al., in review). On the other hand, all specimens of *C. holthuisi* appear within the Malili clade. Therefore, they must be regarded as truly endemic to the lakes. However, within the Malili clade, *C. holthuisi* is not monophyletic, but appears in two allopatric clades (Figs. 10B, 63-64). The existence of two cryptic species is therefore possible despite the fact that morphological differences have not been observed so far.

***Caridina lanceolata* Woltereck, 1937a**  
(Figs. 13-14, Table 6)

*Caridina lanceolata* Woltereck, 1937a: 224, Figs. 1.7a-c, pls. 3,6 (type locality: Lake Towuti at Lingkona, Lake Mahalona)

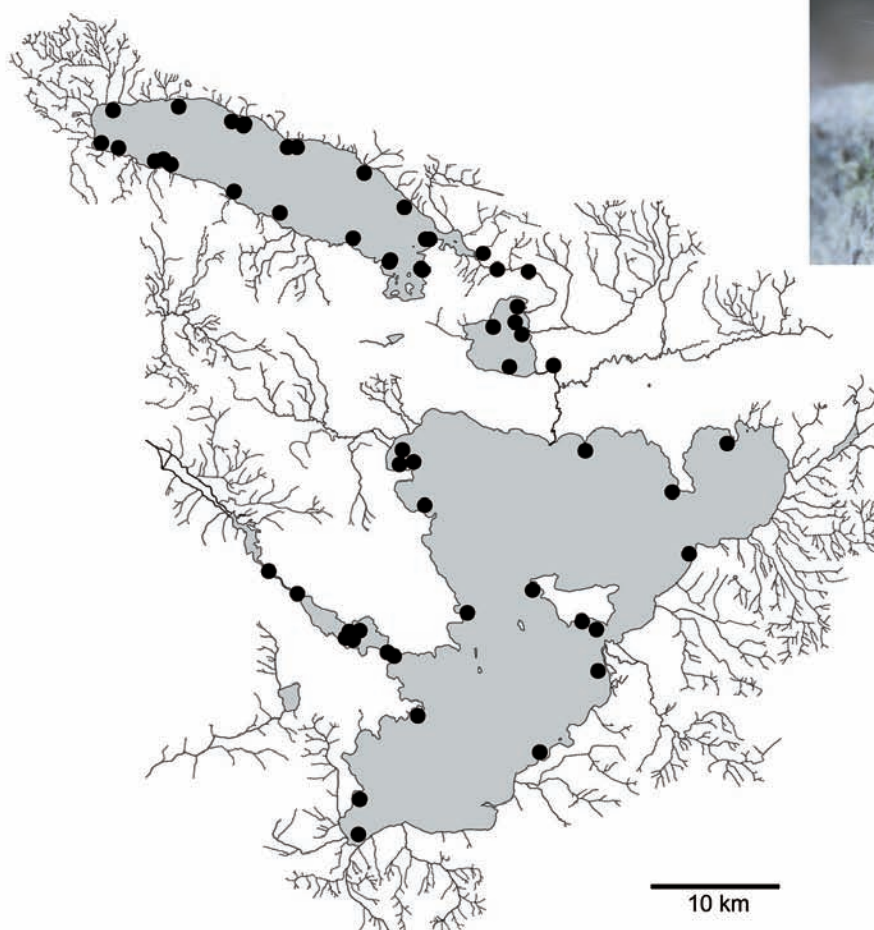
[Mahalona], Lake Matanno [Matano] at Bonti, Lake Matanno at Soroako).

*Caridina lanceolata* – Woltereck, 1937b: 307, fig. 11; Chace, 1997: 12; Fernandez-Leborans et al., 2006a: 1, fig. 24; 2006b: 1985, Table I; Roy et al., 2006: 1090; von Rintelen et al., 2007b: 262, fig. 2b; 2007b: 4, fig. 2, 2008: 2244, Figs. 1, 4, Tables 1, 2; Cai et al., 2009: 15, Figs. 1-2 (type locality of neotype: Lake Matano, Mengonuwai).

*Cardina lanceolata* – Brooks, 1950: 168 (erroneous spelling).

**Material examined.** – Lake Matano: 10 ex. (ZMB 29021, some SEM material), north shore, 02°29.75'S, 121°25.81'E, loc. 42-03, coll. K. & T. von Rintelen, 17 Sep.2003; 112 ex. (MZB Cru 1738, n=55; ZMB 29070, n=57), south shore, at small islands, 02°28.458'S, 121°15.57'E, loc. F4-02, mixed substrate, coll. F. Herder, 2 Nov.2002; 5 ex. (ZMB 29082), northwest corner, 02°27.71'S, 121°13.03'E, loc. 102-03, on rocks in deeper water, coll. K. & T. von Rintelen, 7 Oct.2003; north shore, 02°26.36'S, 121°19.03'E, loc. 84-03, on wood (ZMB 29090, n=3), coll. K. & T. von Rintelen, 1 Oct.2003; 21 ex. (MZB Cru 1739, n=10, ZMB 29110; n=11), south shore, near cave entrance, 02°29.85'S, 121°18.66'E, loc. 60-03, on rocks in deeper water, coll. K. & T. von Rintelen, 24 Sep.2003; 31 ex. (MZB Cru 1740, n=14, ZMB 29111, n=17), south shore, west of small islands, 02°28.5'S, 121°15.55'E, loc. 82-03, on macrophytes, coll. K. & T. von Rintelen, 1 Oct.2003; 129 ex. (MZB Cru 1741a, n=35; ZMB 29120a, n=10 and MZB Cru 1742b, n=50; ZMB 29120b, n=34, some SEM material), north

A.



B.



Fig. 13. *Caridina lanceolata* from the Malili lake system. A. Distribution. B. Colour pattern of living animal (not to scale). Picture courtesy of Chris Lukhaup.

Table 6. Summary of standard morphometric parameters for *Caridina lanceolata*.

parameter	range	mean ± SD	median	n
cl (mm)	2.2-4.0	3.0 ± 0.4	3.1	129
rl / cl	1.5-2.3	1.9 ± 0.2	1.9	120
n dorsal rostral teeth	8-19	14 ± 2	13	124
n ventral rostral teeth	4-13	7 ± 2	7	124
abds6 / cl	0.8-1.1	0.9 ± 0.0	1.0	129
abds6 / abds5	1.4-2.3	2.0 ± 0.1	2.0	33
abds6 / h tel	1.0-1.9	1.3 ± 0.1	1.3	101
h tel / w tel	3.3-3.7	3.5 ± 0.1	3.5	6
n spines uropodal diaeresis	7-9	8 ± 1	8	5
h ch1 / w ch1	1.9-3.5	2.6 ± 0.4	2.6	35
h ch1 / h ca1	0.8-1.4	1.1 ± 0.1	1.1	127
h ca1 / w ca1	2.4-5.3	3.6 ± 0.7	3.7	35
h ch2 / w ch2	2.1-6.7	3.7 ± 0.8	3.7	35
h ch2 / h ca2	0.5-1.6	0.7 ± 0.1	0.6	127
h ca2 / w ca2	5.4-9.9	8.3 ± 1.2	8.6	35
n spines p3	4-6	5 ± 1	6	5
n spines p5	28-35	31 ± 3	31	5

shore, 02°28.42'S, 121°24.21'E, loc. 41-03, (a) on wood, (b) on macrophytes, coll. K. & T. von Rintelen, 17 Sep.2003; 2 ex. (ZMB 29160), west shore, 02°26.828'S, 121°12.988'E, loc. 135-04, on wood, coll. K. & T. von Rintelen & A. Wessel, 23 Jul.2004; 20 ex. (MZB Cru 1743, n=11; ZMB 29162, n=9), south shore, 02°27.84'S, 121°13.88'E, loc. 63-03, on mixed substrate, coll. K. & T. von Rintelen, 24 Sep.2003; 26 ex. (MZB Cru 1744, n=13; ZMB 29164, n=13, some SEM material), east shore, outlet bay, at Petea outlet, 02°32.11'S, 121°28.69'E, loc. 44-03, on macrophytes, coll. K. & T. von Rintelen, 18 Sep.2003; 40 ex. (MZB Cru 1745, n=20; ZMB 29190, n=20), north shore, 02°27.28'S, 121°21.21'E, loc. 98-03, on mixed substrate, coll. K. & T. von Rintelen, 5 Oct.2003; 2 ex. (ZMB 29193), east shore, just south of entrance to outlet bay, 02°31.54'S, 121°27.0'E, loc. 43-03, on rocks in shallow water, coll. K. & T. von Rintelen, 18 Sep.2003; 2 ex. (ZMB 29194), southwest shore, at Cape Nikomene, 02°32.24'S, 121°24.76'E, loc. 46-03, on rocks, coll. K. & T. von Rintelen, 18 Sep.2003; 7 ex. (ZMB 29237), north shore, 02°25.67'S, 121°16.54'E, loc. 65-03, on leaf litter, coll. K. & T. von Rintelen, 25 Sep.2003; 18 ex. (ZMB 29249), south shore, canal between island and mainland, 02°28.46'S, 121°15.83'E, loc. 62-03, on mixed substrate, coll. K. & T. von Rintelen, 1 Oct.2003; 14 ex. (ZMB 29321), south shore, 02°28.461'S, 121°15.591'E, loc. 137-04, on macrophytes, coll. K. & T. von Rintelen, 24 Sep.2004; 2 ex. (ZMB 29322), south shore, at small islands, 02°28.476'S, 121°15.64'E, loc. 138-04, on wood, coll. K. & T. von Rintelen & A. Wessel, 24 Jul.2004; 9 ex. (ZMB 29323), south shore, 02°27.85'S, 121°13.87'E, loc. 125-04, on rocks in deeper water, coll. P. Koller & K. von Rintelen, 1 Aug.2004; 1 ex. (MZB Cru 1746), east shore, south bay, 02°32.77'S, 121°26.71'E, loc. 45-03, on rocks, coll. K. & T. von Rintelen, 18 Sep.2003; 1 ex. (ZMB 29188), Petea River, 02°32.64'S, 121°29.51'E, loc. 101-03, on leaf litter, coll. K. & T. von Rintelen, 6 Oct.2003; 15 ex. (MZB Cru 1762, n=8; ZMB 29279, n=7), Petea River, 02°32.672'S, 121°30.137'E, loc. F4-04, substrate unknown, coll. F. Herder, 25 Mar.2004.

Lake Mahalona – 41 ex. (MZB Cru 1747a, n=2; ZMB 29022a, n=21 and MZB Cru 1748b, n=9; ZMB 29022b, n=9, some SEM material), northwest shore, 02°34.72'S, 121°29.12'E, loc. 56-03, on (a) on wood, (b) on macrophytes, coll. K. & T. von Rintelen, 23 Sep.2003; 22 ex. (MZB Cru 1749, n= 11; ZMB 29041, n=11),

east shore, 02°34.54'S, 121°30.48'E, loc. 55-03, on *Ottelia*, coll. K. & T. von Rintelen, 23 Sep.2003; 12 ex. (MZB Cru 1750, n=6; ZMB 29042, n=6, some SEM material), south shore, 02°36.93'S, 121°30.02'E, loc. 57-03, on *Ottelia*, coll. K. & T. von Rintelen, 23 Sep.2003; 18 ex. (MZB Cru 1751, n=9; ZMB 29236; n=9, some SEM material), east shore, 02°34.217'S, 121°30.681'E, loc. 147-04, on macrophytes, coll. K. & T. von Rintelen, 3 Aug.2004; 31 ex. (MZB Cru 1752, n=15; ZMB 29250, n=16), south shore, 02°36.982'S, 121°30.078'E, loc. 45-04, on wood, coll. M. Glaubrecht & T. von Rintelen, 26 Mar.2004; 1 ex. (ZMB 29336), north shore, at cape, 02°34.71'S, 121°29.144'E, loc. 148-04, on mixed substrate, coll. K. & T. von Rintelen, 3 Aug.2004; 15 ex. (MZB Cru 1753), east shore, estuary of Ponsoa River, 02°35.101'S, 121°30.681'E, loc. 146-04, on *Ottelia*, coll. P. Koller, K. & T. von Rintelen, 3 Aug.2004; 8 ex. (ZMB 29115), Tominanga River, approx. 2.2 km north of Lake Towuti, 02°36.5'S, 121°31.78'E, loc. 58-03, on macrophytes, coll. K. & T. von Rintelen, 23 Sep.2003.

Lake Towuti – 69 ex. (MZB Cru 1754, n=59; ZMB 29029, n=10, some SEM material), south shore, approx. 100 m offshore, 02°56.27'S, 121°23.67'E, loc. 75-03, on *Ottelia*, coll. K. & T. von Rintelen, 28 Sep.2003; 2 ex. (ZMB 29030), west shore, 02°48.526'S, 121°25.044'E, loc. 120-04, on wood, coll. K. & T. von Rintelen & A. Wessel, 29 Jul.2004; 141 ex. (MZB Cru 1755, n=123; ZMB 29032, n=18, some SEM material), west shore, outlet bay, east of Cape Kombe, 02°48.08'S, 121°23.05'E, loc. 53-03, on mixed substrate, coll. K. & T. von Rintelen, 21 Sep.2003; 34 ex. (MZB Cru 1756, n=24; ZMB 29033a, n=8 and ZMB 29033b, n=2, some SEM material), southwest shore, Cape Sioloya, 02°50.7'S, 121°26.32'E, loc. 77-03, (MZB and ZMB a) pelagic, (b) on wood, coll. K. & T. von Rintelen, 28 Sep.2003; 3 ex. (ZMB 29081), east shore, south of Cape Tomeraka, 02°44.47'S, 121°37.53'E, loc. 70-03, on rocks, coll. K. & T. von Rintelen, 9 Oct.2003; 206 ex. (MZB Cru 1757a, n=22; ZMB 29093a, n=11 and MZB Cru 1758b, n=92; ZMB 29093b, n=81, some SEM material), southwest shore, west of Cape Tetetu, 02°45.13'S, 121°23.78'E, loc. 76-03, (a) on wood, (b) pelagic, coll. K. & T. von Rintelen, 28 Sep.2003; 10 ex. (ZMB 29094, some SEM material), northeast shore, at Cape Nooto, 02°39.751'S, 121°39.195'E, loc. 117-04, on wood, coll. K. & T. von Rintelen, 28 Jul.2004; 7 ex. (ZMB 29112), Loeha Island, south

shore, 02°46.85'S, 121°32.86'E, loc. 96-03, on macrophytes, coll. K. & T. von Rintelen, 4 Oct.2003; 9 ex. (ZMB 29113), east shore, off Beau village, 02°48.99'S, 121°33.64'E, loc. 71-03, on *Ottelia*, coll. K. & T. von Rintelen, 27 Sep.2003; 55 ex. (MZB Cru 1759, n=27; ZMB 29114, n=28), west shore, outlet bay, west of Cape Tokaluku, 02°47.32'S, 121°23.38'E, loc. 52-03, on macrophytes, coll. K. & T. von Rintelen, 21 Sep.2003; 1 ex. (ZMB 29128), west shore, at entrance to outlet bay, Cape Larona, 02°48.43'S, 121°24.75'E, loc. 73-03, on wood, coll. K. & T. von Rintelen, 27 Sep.2003; (ZMB 29158, few juveniles), north shore, west of Cape Manu, 02°41.67'S, 121°36.85'E, loc. 69-03, on macrophytes, coll. K. & T. von Rintelen, 27 Sep.2003; 4 ex. (ZMB 29161), Larona River, close to outlet bay, 02°45.8'S, 121°20.8'E, loc. 51-03, on macrophytes, coll. K. & T. von Rintelen, 21 Sep.2003; 13 ex. (MZB Cru 1761, n=6; ZMB 29163, n=7), Larona River, close to outlet bay, 02°45.6'S, 121°20.12'E, loc. 50-03, on macrophytes, coll. K. & T. von Rintelen, 20 Sep.2003; (ZMB 29166, few juveniles), east shore, 02°52.79'S, 121°31.18'E, loc. 72-03, on *Ottelia*, coll. K. & T. von Rintelen, 27 Sep.2003; 7 ex. (ZMB 29167), Loeha Island, south shore, 02°47.22'S, 121°33.68'E, loc. 91-03, on *Ottelia*, coll. K. & T. von Rintelen, 2 Oct.2003; 12 ex. (ZMB 29181), Loeha Island, west shore, 02°45.5'S, 121°31.06'E, loc. 95-03, on rocks, coll. K. & T. von Rintelen, 4 Oct.2003; 23 ex. (ZMB 29182, some SEM material), north shore, bay east of Cape Bintu, 02°39.48'S, 121°33.25'E, loc. 68-03, on rocks, coll. K. & T. von Rintelen, 26 Sep.2003; (ZMB 29183, few juveniles) west shore, north of Cape Wasupute, 02°46.9'S, 121°27.94'E, loc. 78-03, on rocks, coll. K. & T. von Rintelen, 28 Sep.2003; 4 ex. (ZMB 29314), west shore, outlet bay, 02°47.142'S, 121°23.63'E, loc. 11-05, on mixed substrate, coll. K. & T. von Rintelen, 9 Jan.2005; 4 ex. (ZMB 29315), west shore, Cape Bakara, 02°40.771'S, 121°26.11'E, loc. 144-04, on mixed substrate, coll. K. & T. von Rintelen, 26 Jul.2004; 12 ex. (ZMB 29317), west shore, west of Cape Timbalo, 02°42.631'S, 121°26.389'E, loc. 145-04, on wood, coll. K. & T. von Rintelen, 26 Jul.2004; 4 ex. (ZMB 29318), northwest shore, south of Timampu, 02°39.466'S, 121°25.859'E, loc. 140-04, on macrophytes, coll. K. & T. von Rintelen, 25 Jul.2004; 43 ex. (MZB Cru 1760, n= 28; ZMB 29319, n=15), outlet bay, at Cape Kombe, 02°48.083'S, 121°23.049'E, loc. 118-04, (MZB) on macrophytes, (ZMB) on wood, coll. K. & T. von Rintelen, 29 Jul.2004; 8 ex. (ZMB 29320), northwest shore, 02°40.897'S, 121°25.015'E, loc. 143-04, on wood (*Pandanus*), coll. K. & T. von Rintelen, 25 Jul.2004.

**Description.** – Carapace length 2.2-4.0 mm (n=129). Rostrum (Fig. 14A-C; Table 6) very long, slender and always strongly upturned, reaching far beyond end of scaphocerite, 1.5-2.3 times as long as carapace (n=120), armed dorsally with 8-19 teeth (including 1-3 teeth posterior to orbital margin), approx. anterior third to half unarmed, usually with 1-4 subapical teeth, sometimes subapical teeth absent, armed ventrally with 4-13 teeth (n=124). Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.6-0.7 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.9-1.0 times as long as carapace (n=5), second segment 2.0-2.4 times length of third segment, third segment 0.2-0.3 times length of basal segment. Stylocerite reaching 0.87-0.9 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 14F) 4.8-5.4 times as long as wide (n=5).

Sixth abdominal somite 0.8-1.1 times length of carapace (n=129), 1.4-2.3 times as long as fifth somite (n=33), 1.0-1.9 times length of telson (n=101). Telson (Fig. 14G,J)

3.3-3.7 times as long as wide (n=6), distal margin rounded, without projection, with 3-5 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 4 pairs of spines, lateral pair distinctly longer than intermediate pairs, median pair shortest. Preanal carina (Fig. 14E) with a spine. Uropodal diaeresis (Fig. 14D) with 7-9 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair of podobranchs on second arthrobranch maxillipeds reduced strongly to a laminate form. Epipods only present on first two pereopods. Mouthparts as described by Cai et al. (2009).

Chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig. 14M-O); chela of first pereopod 1.9-3.5 times as long as wide (n=35), 0.8-1.4 times length of carpus (n=127); tips of fingers rounded, without hooks; dactylus 1.2-1.5 times as long as palm (n=7); carpus 2.4-5.3 times as long as wide (n=35), 1.2-1.4 times length of merus (n=5). Chela of second pereopod 2.1-6.7 times as long as wide (n=35), 0.5-1.6 times length of carpus (n=127); tips of fingers rounded, without hooks, dactylus 1.2-1.7 times as long as palm (n=7); carpus 5.4-9.9 times as long as wide (n=35), 1.5-1.6 times as long as merus (n=5).

Third pereopod (Fig. 14H,K) slender, dactylus 4.5-5.4 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 4-6 accessory spines on flexor margin; propodus 12.3-18.8 times as long as wide, 3.4-4.5 times as long as dactylus; carpus 5.8-6.8 times as long as wide, 0.5 times as long as propodus, 0.5 times as long as merus; merus 10.5-11.4 times as long as wide, bearing 3-4 strong, movable spines on posterior margin of outer surface.

Fifth pereopod slender (Fig. 14I,L), dactylus 4.0-6.2 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 28-35 accessory spines on flexor margin; propodus 11.3-21.3 times as long as wide (n=5), 3.3-5.3 times as long as dactylus; carpus 5.0-6.3 times as long as wide, 0.5 times as long as propodus, 0.5-0.6 times as long as merus; merus 8.3-11.5 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 14P) elongated triangular, 1.4-2.5 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 14Q) 0.9-1.0 times length of appendix masculina (n=5).

Ovigerous females with 15-69 eggs (n=27 females); egg size 0.6-0.9 x 0.4-0.6 mm (n=701, eggs with and without eyes).

**Distribution.** – Endemic to the Malili lake system, widely distributed and abundant in Lake Matano, Lake Mahalona, Lake Towuti, and connecting rivers, i.e. Larona (close to the

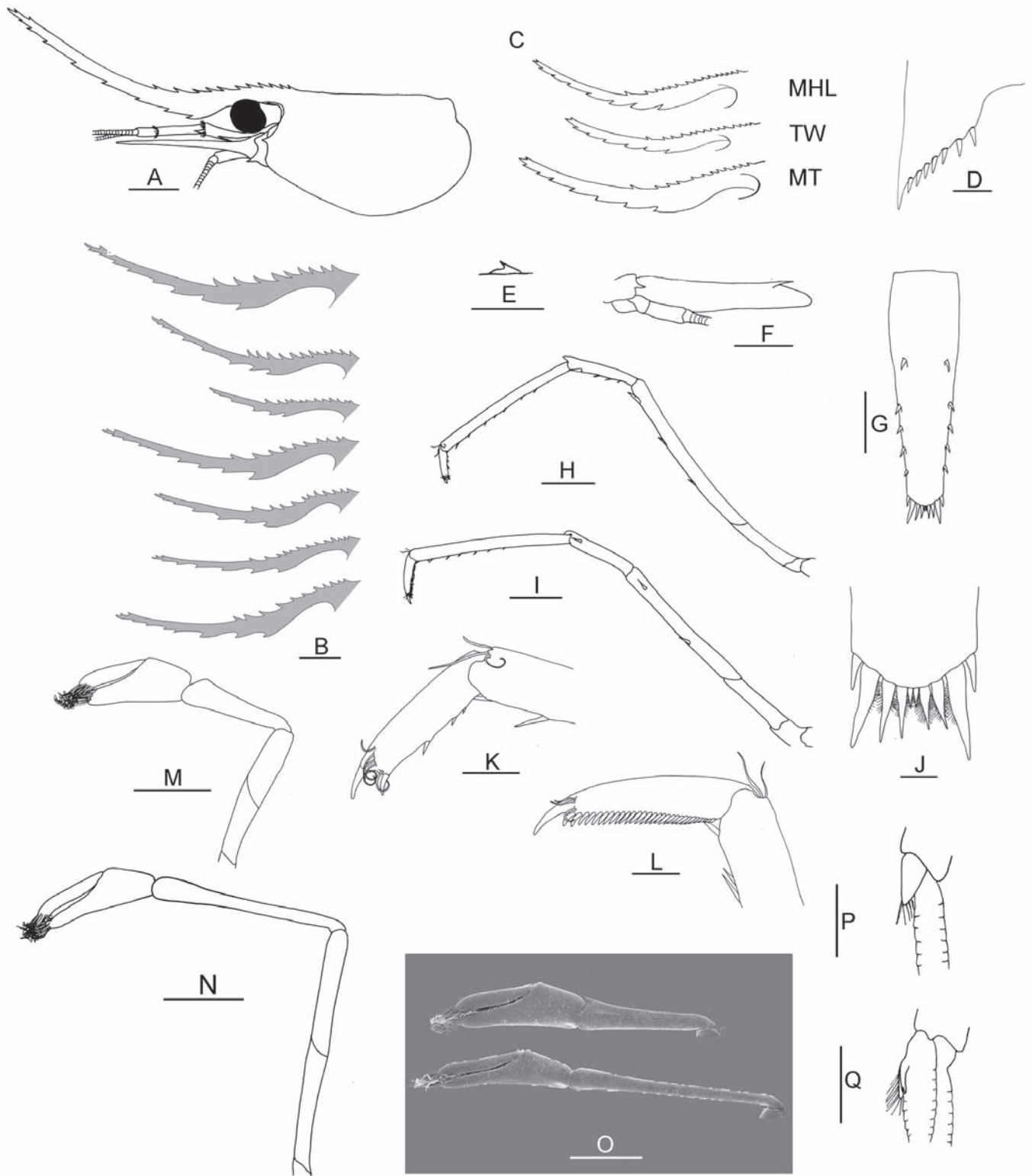


Fig. 14. *Caridina lanceolata* from the Malili lake system. A. Cephalothorax and cephalic appendages, female (ZMB 29032); B. Rostrum variability (ZMB 29033a); C. Woltereck's drawings of the rostrum, from several lakes (modified from 1937a); D. Uropodal diaeresis, female (ZMB 29032); E. Preanal carina, male (ZMB 29093a), F. Scaphocerite; G. Telson, female (ZMB 29032); H. Third pereiopod, female (ZMB 29093b); I. Fifth pereiopod; J. Distal end of telson, female (ZMB 29032); K. Dactylus of third pereiopod, female (ZMB 29093b); L. Dactylus of fifth; M. first pereiopod, female (ZMB 29032); N. Second pereiopod; O. SEM image of chela and carpus of first and second pereiopods; P. Endopod of male first pleopod (ZMB 29093a); Q. Appendix masculina of male second pleopod. Scale bars: A-B, F = 1.0 mm; E, G-I, M-Q = 0.5 mm; D, J-L = 0.1 mm; C = no scale available.

outlet of Lake Towuti), Petea, and Tominanga (Fig. 13A). As these rivers are rather an extension of the lakes themselves (albeit with currents), *C. lanceolata* is regarded here, in contrast to *C. masapi*, as a typical lacustrine species.

**Biology and ecology.** – *C. lanceolata* occurs on various kinds of substrates, except sponges, that are available in the Malili lakes (rocks from gravel to boulders, wood, leaf litter, different kinds of macrophytes, and in pelagic swarms), and down to a depth of approx. 10 m. When disturbed, *C. lanceolata* makes characteristic abrupt movements in all directions or simply keeps still in midwater. It often occurs syntopically, i.e. on the same substrate, with other species, for example with *C. tenuirostris* on wood in Lake Towuti and Lake Mahalona. It is the only wood dweller in Lake Matano and often the only shrimp on macrophytes surrounded by sand or mud, e.g. on the basal parts of the water plant *Ottelia*.

**Colour pattern.** – Body and appendages are transparent throughout, with a reddish pigmentation caused by several red, sometimes yellowish-greenish, dots or spots (Fig. 13B). Ovipigerous females were observed to bear green eggs.

**Taxonomic remarks.** – Cai et al. (2009: 19) designated a neotype for *C. lanceolata*: “Specimens of Woltereck (1937a, b) are no longer extant [...]. As all new species described by Woltereck are morphologically close to each other and to stabilize the taxonomic status of those species, neotypes are designated if specimens are available from the recent collections. A neotype from Lake Towuti is designated here (1 male, cl 2.9 mm, ZRC, Lake Matano, south coast)”.

*C. lanceolata* can easily be distinguished from all other ancient lake species by the characteristic shape and denticulation of the rostrum, which is already visible in juveniles: strongly upturned with approximately anterior third to half unarmed and usually with 1-4 subapical teeth. The arrangement of rostral teeth slightly resembles *C. tenuirostris*, but this species has a distinctly more slender rostrum, a higher number of ventral teeth (10-24, median 15 vs. 4-13, median 7 in *C. lanceolata*), and subapical teeth are always absent. Also, *C. lanceolata* differs from all other species by a distinctly longer sixth abdominal somite compared to the carapace length (0.8-1.1, median 1.0 vs. shorter in all other species).

Roy et al. (2006) hint at the possibility that *C. lanceolata* might comprise cryptic species, but a recent study by von Rintelen et al. (in review) does not support this hypothesis. Although there are genetic differences between allopatric populations from the three major lakes of the Malili system, *C. lanceolata* is here regarded as a valid taxon without the need of further taxonomic subdivision. *C. lanceolata* is genetically distinct from all other ancient lakes species (Figs. 63-64), and the clade only consisting of *C. lanceolata* specimens even represents a single colonization event of the Malili lakes (Fig. 63).

### *Caridina lingkonae* Woltereck, 1937a

(Figs. 15-17, Table 7)

*Caridina Lingkonae* Woltereck, 1937a: 218, fig. I.1, pls. 3,6 (type locality: Lake Towuti at Loéha Island and at Lingkona [Lengkona]).

*Caridina lingkonae* – Woltereck, 1937b: 299, fig. 6; Chace, 1997: 13; von Rintelen et al., 2008: 2244, Table 1.

*Cardina lingkonae* – Brooks, 1950: 168 (erroneous spelling).

*Caridina linkonae* – Fernandez-Leborans et al., 2006b: 1985, Table I (erroneous spelling).

**Material examined.** – Neotype: ovigerous female (cl. 4.1 mm)(MZB Cru. 1554), Lake Towuti, west shore, at entrance to outlet bay, Cape Larona, 02°48.43'S, 121°24.75'E, loc. 73-03, pelagic, coll. K. & T. von Rintelen, 27 Sep.2003.

Others from Lake Towuti: 184 ex. (MZB Cru 1763, n=149; ZMB 29076, n=35, some SEM material), west shore, at entrance to outlet bay, Cape Larona, 02°48.43'S, 121°24.75'E, loc. 73-03, pelagic, coll. K. & T. von Rintelen, 27 Sep.2003; 18 ex. (MZB Cru 1764, n=9; ZMB 29235, n=9), southwest shore, west of Cape Tetetu, 02°54.13'S, 121°23.78'E, loc. 76-03, pelagic, coll. K. & T. von Rintelen, 28 Sep.2003; 1 ex. (ZMB 29239), east shore, south of Cape Tomeraka, 02°44.47'S, 121°37.53'E, loc. 70-03, on rocks, coll. K. & T. von Rintelen, 9 Oct.2003; 1 ex. (ZMB 29282), west shore, Cape Larona, 02°48.526'S, 121°25.044'E, loc. 120-04, boulders in deeper water, coll. K. & T. von Rintelen, 29 Jul.2004; 3 ex. (ZMB 29283), west shore, west of Cape Timbalo, 02°42.631'S, 121°26.389'E, loc. 145-04, on mixed substrate, coll. K. & T. von Rintelen, 26 Jul.2004; 1 ex. (ZMB 29287), outlet bay, at Cape Kombe, 02°48.083'S, 121°23.049'E, loc. 118-04, on boulders in deeper water, coll. K. & T. von Rintelen, 29 Jul.2004; 15 ex. (MZB Cru 1765, n=7; ZMB 29302, n=8), northeast shore, at Lengkona, 02°40.483'S, 121°41.382'E, loc. 116-04, on mixed substrate, coll. K. & T. von Rintelen, 28 Jul.2004; 3 ex. (ZMB 29304), Loeha Island, west shore, 02°45.5'S, 121°31.06'E, loc. 951-03, on rocks, coll. K. & T. von Rintelen, 4 Oct.2003; 1 ex. (ZMB 29316), northeast shore, at Cape Noote, 02°39.751'S, 121°39.195'E, loc. 117-04, pelagic, coll. K. & T. von Rintelen, 28 Jul.2004; 3 ex. (MZB Cru 1766), west shore, outlet bay, 02°46.277'S, 121°21.83'E, loc. 02-05, on sponge, coll. K. & T. von Rintelen, 3 Jan.2005; 7 ex. (MZB Cru 1767), east shore, off Beau village, 02°48.99'S, 121°33.64'E, loc. 71-03, on *Ottelia*, coll. K. & T. von Rintelen, 27 Sep.2003.

Others from Lake Mahalona: 1 ex. (ZMB 29208), east shore, at mouth of Petea River, 02°34.54'S, 121°30.48'E, loc. 55-03, on leaf litter, coll. K. & T. von Rintelen, 23 Sep.2003.

**Description.** – Carapace length 2.3-4.5 mm (n=46). Rostrum (Fig. 16A-B; Table 7) long, reaching beyond end of scaphocerite, proximal part typically triangular, 1.0-1.6 times as long as carapace (n=46), armed dorsally with 17-29 teeth (including 3-5 teeth posterior to orbital margin), anteriorly less densely spaced, armed ventrally with 7-18 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.6-0.7 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.9-1.2 times as long as carapace (n=5), second segment 1.7-2.0 times length of third segment, third segment 0.3-0.4 times length of basal segment. Stylocerite reaching 0.8-0.9 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 16F) 4.1-5.3 times as long as wide (n=5).

Sixth abdominal somite 0.7-0.9 times length of carapace (n=46), 1.6-1.9 times as long as fifth somite (n=20), 1.0-1.3 times length of telson (n=26). Telson (Fig. 16D,K) 3.4-3.6 times as long as wide (n=5), distal margin rounded, without projection, with 3-4 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 4 pairs of spines, lateral pair distinctly longer than intermediate pairs, median pair shortest. Preanal carina (Fig. 16E) with a spine. Uropodal diaeresis (Fig. 16C) with 9-11 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipod reduced or absent from first pereopod. Incisor process of mandible (Fig. 17A) ending in a row of small teeth, molar process truncated. Lower lacinia of maxillula (Fig. 17B) broadly rounded, upper lacinia elongate, with numerous distinct teeth on inner margin, palp slender. Upper endites of maxilla (Fig. 17C) subdivided, palp short, scaphognathite tapering posteriorly with numerous long, curved setae at posterior end. Distal end of palp of first maxilliped (Fig. 17F) triangular, with a finger-like projection;

flagellum of the exopod very short, endopod high, distinctly exceed the flagellum of exopod in length. Second maxilliped (Fig. 17E) typical. Third maxilliped (Fig. 17D) with ultimate segment distinctly shorter than penultimate segment.

First and second pereopod very slender, chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig. 16N-P); chela of first pereopod 3.0-4.1 times as long as wide (n=20), 0.9-1.1 times length of carpus (n=46); tips of fingers rounded, without hooks; dactylus 1.7-1.9 times as long as palm (n=5); carpus 4.4-5.0 times as long as wide (n=20), 1.3-1.4 times length of merus (n=5). Chela of second pereopod 4.2-5.6 times as long as wide (n=20), 0.6-0.8 times length of carpus (n=46); tips of fingers rounded, without hooks, dactylus 1.4-1.6 times as long as palm (n=5); carpus 7.9-10.7 times as long as wide (n=20), 1.6-1.7 times as long as merus (n=5).

Third pereopod (Fig. 16G,I) slender, dactylus 4.3-5.5 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 1-3 accessory spines on flexor margin; propodus 13.2-17.0 times as long as wide, 3.9-4.9 times as long as dactylus;

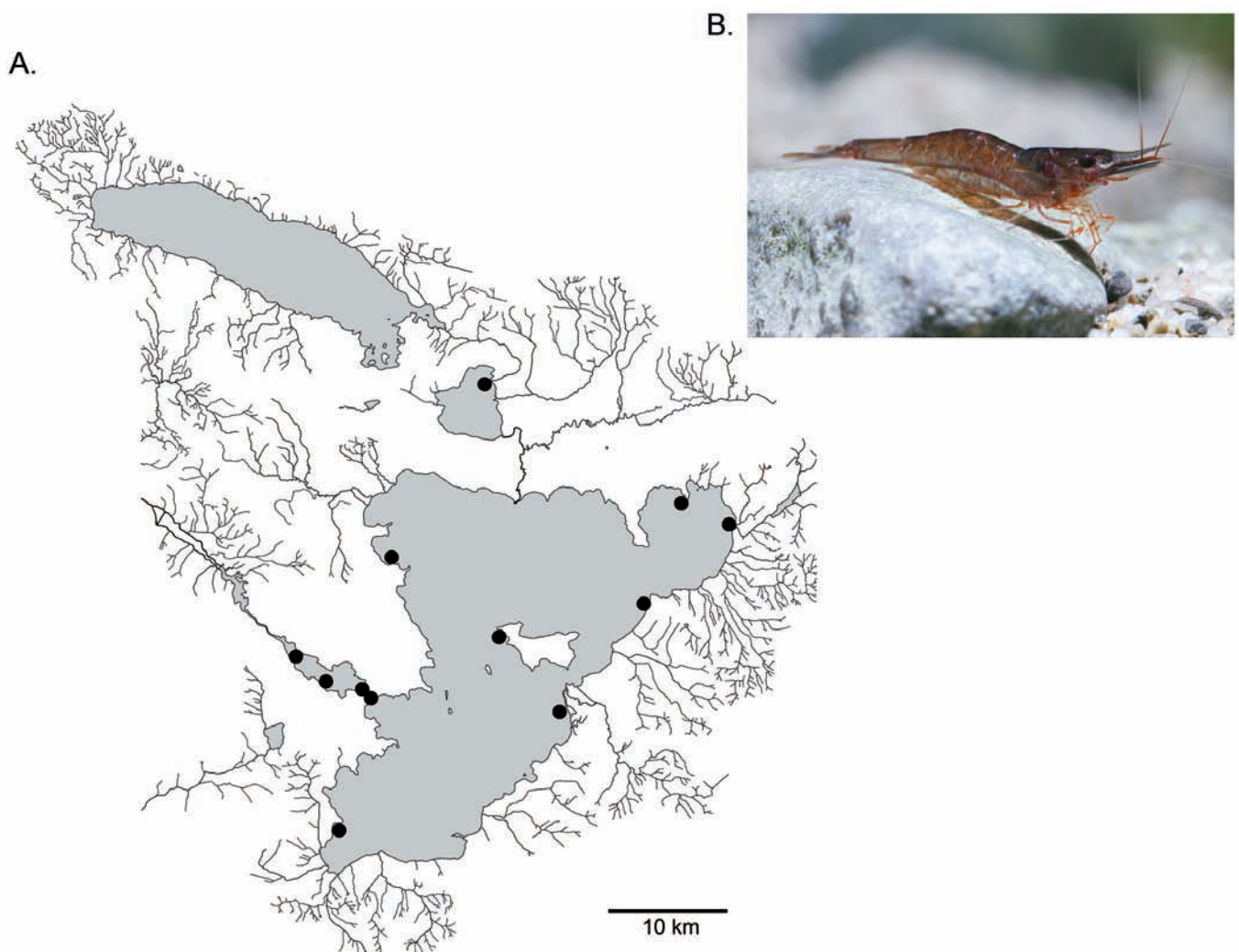


Fig. 15. *Caridina lingkonae* from the Malili lake system. A. Distribution. B. Colour pattern of living animal (not to scale). Picture courtesy of Chris Lukhaup.



Table 7. Summary of standard morphometric parameters for *Caridina lingkonae*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	2.3-4.5	3.5 $\pm$ 0.6	3.6	46
rl / cl	1.0-1.6	1.3 $\pm$ 0.1	1.2	46
n dorsal rostral teeth	17-29	22 $\pm$ 3	22	46
n ventral rostral teeth	7-18	12 $\pm$ 2	12	46
abds6 / cl	0.7-0.9	0.8 $\pm$ 0.1	0.8	46
abds6 / abds5	1.6-1.9	1.8 $\pm$ 0.1	1.8	20
abds6 / h tel	1.0-1.3	1.1-0.1	1.1	26
h tel / w tel	3.4-3.6	3.5 $\pm$ 0.1	3.5	5
n spines uropodal diaeresis	9-11	10 $\pm$ 1	10	5
h ch1 / w ch1	3.0-4.1	3.5 $\pm$ 0.3	3.5	20
h ch1 / h ca1	0.9-1.1	1.0 $\pm$ 0.1	1.0	46
h ca1 / w ca1	4.4-5.0	4.7-0.2	4.7	20
h ch2 / w ch2	4.2-5.6	4.8 $\pm$ 0.3	4.8	20
h ch2 / h ca2	0.6-0.8	0.7 $\pm$ 0.0	0.7	46
h ca2 / w ca2	7.9-10.7	9.6 $\pm$ 0.7	9.6	20
n spines p3	1-3	2 $\pm$ 1	1	5
n spines p5	17-42	33 $\pm$ 10	36	5

carpus 5.3-5.9 times as long as wide, 0.5 times as long as propodus, 0.4-0.5 times as long as merus; merus 10.5-12.2 times as long as wide, bearing 3-4 strong, movable spines on posterior margin of outer surface.

Fifth pereopod slender (Fig. 16H,J), dactylus 3.5-5.6 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 17-42 accessory spines on flexor margin; propodus 14.0-19.3 times as long as wide, 4.3-5.5 times as long as dactylus; carpus 5.3-6.1 times as long as wide, 0.4-0.6 times as long as propodus, 0.5-0.6 times as long as merus; merus 10.0-12.4 times as long as wide, bearing 2-5 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 16L) elongated triangular, 2.0-2.5 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 16M) 0.8-0.9 times length of appendix masculina (n=5).

Ovigerous females with 30-32 eggs (n=3 females); egg size 0.7-1.0 x 0.4-0.6 mm (n=90, eggs with and without eyes).

**Distribution.** – Endemic to the Malili lakes, widely distributed in Lake Towuti, a single specimen was caught in Lake Mahalona (Fig. 15A).

**Biology and ecology.** – *Caridina lingkonae* was already mentioned as littoral and pelagic by Woltereck (1937a: 229) and Brooks (1950: 168). The majority of the specimens caught between 2003 and 2004 were found in huge pelagic swarms similarly to those of *C. ensifera* from Lake Poso. Although it was likewise found sporadically on other substrates (e.g. rocks or leaf litter), *C. lingkonae* is here regarded as a typical pelagic species. In comparison, *C.*

*lanceolata* was also found in occasionally pelagic swarms, but the majority of specimens of that species occurred in the littoral on various kind of substrate. When disturbed, it tries to escape in all directions.

**Colour pattern.** – *C. lingkonae* has a translucent reddish body colouration throughout, similarly to *C. lanceolata*, but more pronounced (Fig. 15B). Ovigerous females bear green eggs.

**Taxonomic remarks.** – *C. lingkonae* might be confused with *C. lanceolata* in the field, especially when occurring as a pelagic swarm, but a generally stouter body and the typical triangular shape of the rostrum (vs. not triangular, but longer and more slender in *C. lanceolata*) are characteristic for this species. *C. lingkonae* can further be distinguished by the dorsal denticulation of the rostrum (17-29 continuous teeth vs. 8-19 teeth including an unarmed gap in *C. lanceolata*) and a shorter sixth abdominal segment compared to the carapace length (0.7-0.9, median 0.8 vs. 0.8-1.1, median 1.0 in *C. lanceolata*). The typical triangular shape of the proximal part of the rostrum (best visible transilluminated), and its dense dorsal and ventral denticulation in *C. lingkonae*, has already been mentioned by Woltereck (1937a: 218,b: 299). A similarly triangular shape is pronounced in *C. profundicola*, but this species differs from *C. lingkonae* by a distinctly more slender and also longer rostrum compared to carapace length (1.4-2.8, median 1.9 vs. 1.0-1.6, median 1.2 in *C. lingkonae*) and a higher number of ventral teeth (13-24, median 20 vs. 7-18, median 12 in *C. lingkonae*). *C. lingkonae* has similarly slender pereopods than *C. profundicola* and *C. spinata* that further distinguish *C. lingkonae* from all other species. Furthermore, *C. lingkonae* differs from *C. spinata* by the shape of the rostrum and less spines on the uropodal diaeresis; 9-11, median 10 vs. 12-16, median 14 in *C. spinata*).

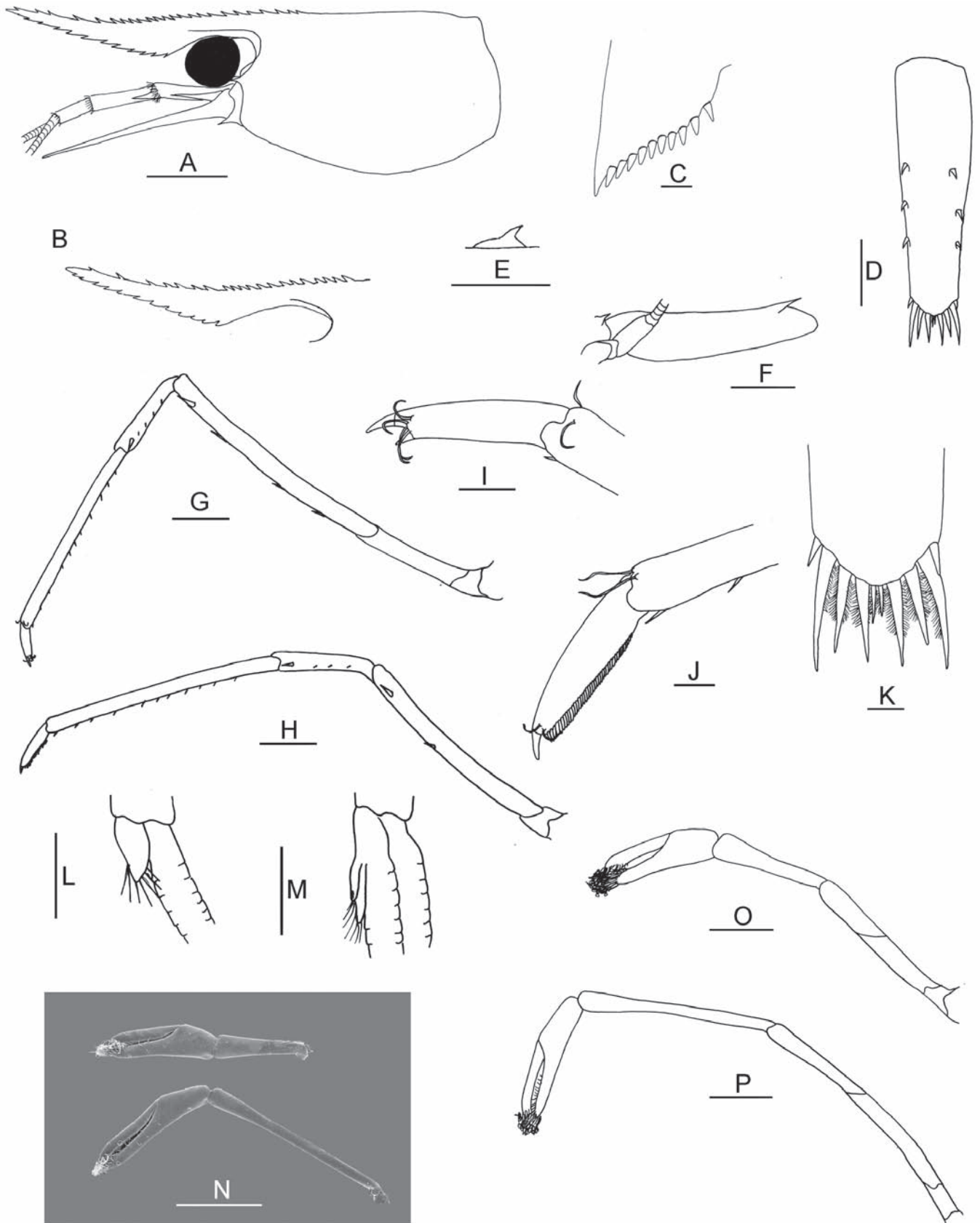


Fig. 16. *Caridina lingkonae* from the Malili lake system. A. Cephalothorax and cephalic appendages, female (ZMB 29076); B. Woltereck's drawings of the rostrum, Lake Towuti (modified from 1937a); C. Uropodal diaeresis, female (ZMB 29076); D. Telson; E. Preanal carina, male (ZMB 29076); F. Scaphocerite; G. Third pereiopod, female (ZMB 29076); H. Fifth pereiopod; I. Dactylus of third pereiopod; J. Dactylus of fifth pereiopod; K. Distal end of telson; L. Endopod of male first pleopod (ZMB 29076); M. Appendix masculina of male second pleopod; N. SEM image of chela and carpus of first and second pereiopods; O. First pereiopod; P. Second pereiopod. Scale bars: A, F = 1.0 mm; D-E, G-H, L-P = 0.5 mm; C, I-K = 0.1 mm; B = no scale available.

In the molecular phylogeny (Figs. 63-64), *C. lingkonae* is genetically distinct from all ancient lake species.

*Caridina loehae* Woltereck, 1937a  
(Figs. 18-19, Table 8)

*Caridina Loéhae* Woltereck, 1937a: 222, Figs. I.5a-d, pls. 3,6 (type locality: Matanno [Matano] islands, Lake Towuti XX, Lake Towuti at Loéha Island and at Lingkona).

*Caridina loéhae* – Woltereck, 1937b: 304, fig. 9; Fernandez-Leborans et al., 2006b: 1985, Table I (partly as *C. loeha*, erroneous spelling).

*Caridina loehae* – Chace, 1997: 13; von Rintelen et al., 2008: 2244, Table 1; Cai et al., 2009: 27, Fig. 7 (type locality of neotype: Lake Towuti, about 3 km south of Timampu, estuary of Sungei [River] Batuopa).

*Cardina loéhae* – Brooks, 1950: 168 (erroneous spelling).

**Material examined.** – Lake Matano: 8 ex. (ZMB 29062, n=8), north shore, 02°26.36'S, 121°19.03'E, loc. 84-03, on rocks, coll.

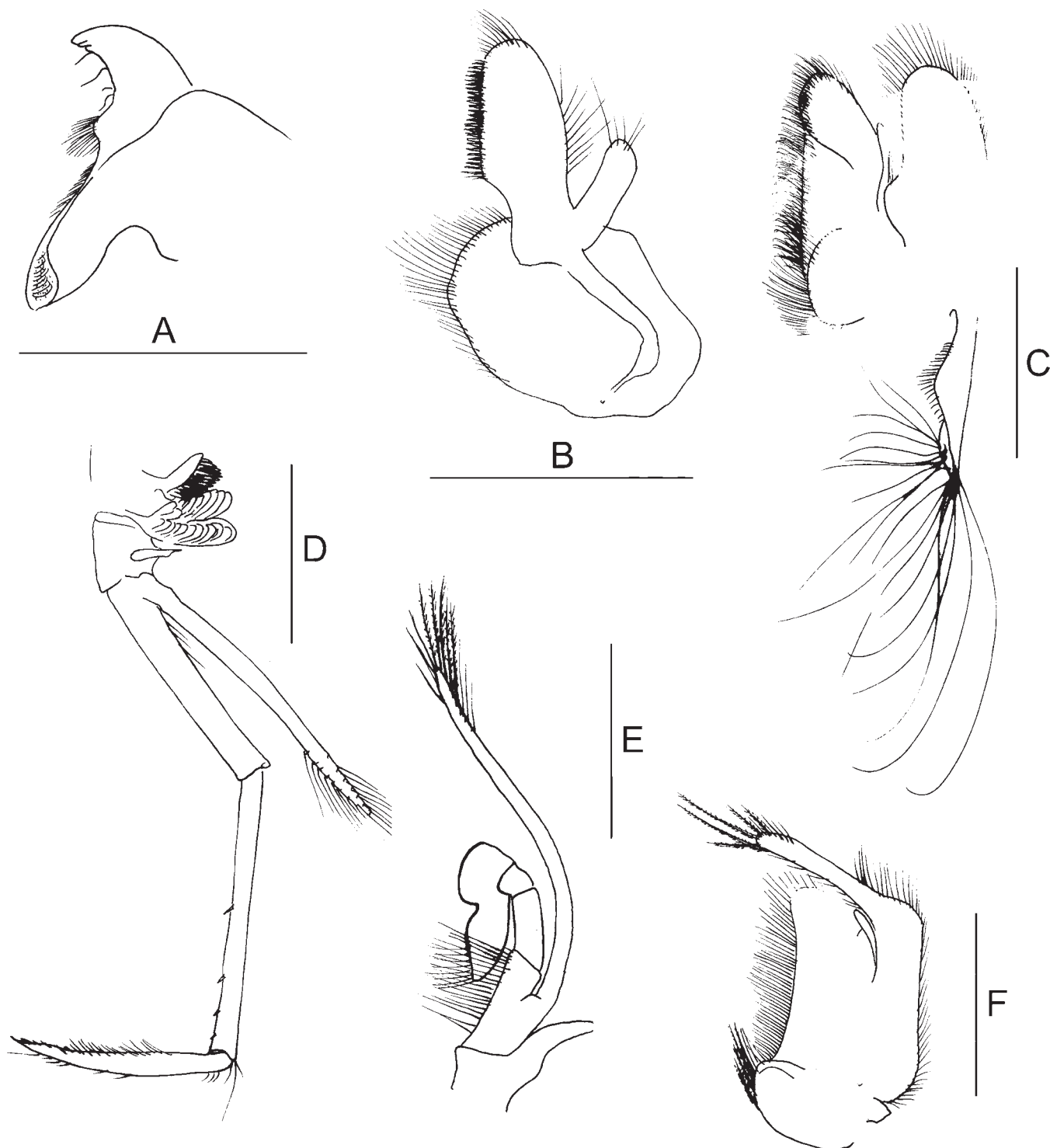


Fig. 17. *Caridina lingkonae* from the Malili lake system. A. Mandible (ZMB 29076); B. Maxillula; C. Maxilla; D. third maxilliped; E. second maxilliped; F. first maxilliped. Scale bars: A-F = 1mm.

K. & T. von Rintelen, 1 Oct.2003; 20 ex. (MZB Cru 1768, n=10; ZMB 29066, n=10, some SEM material), north shore, 02°27.28'S, 121°21.21'E, loc. 98-03, on rocks, coll. K. & T. von Rintelen, 5 Oct.2003; 3 ex. (ZMB 29079, and few juveniles), south shore, Soroako, Salonsa, INCO boat house, 02°30.71'S, 121°20.45'E, loc. 04-05, on rocks, coll. K. & T. von Rintelen, 3 Jan.2005; 42 ex. (MZB Cru 1769, n=30, ZMB 29080, n=12, some SEM material), south shore, Soroako, Salonsa, INCO boat house, 02°30.71'S, 121°20.45'E, loc. 19-03, on rocks, coll. K. & T. von Rintelen, 19 Sep.2003; 15 ex. (MZB Cru 1770, n=7; ZMB 29118, n=8, some SEM material), south shore, east of Soroako, just west of Cape Patipuoho, 02°31.57'S, 121°23.41'E, loc. 99-03, on rocks, coll. K. & T. von Rintelen, 5 Oct.2003; 4 ex. (ZMB 29233, some SEM material), southwest shore, Cape Nikomene, 02°32.24'S, 121°24.76'E, loc. 46-03, on rocks, coll. K. & T. von Rintelen, 18 Sep.2003; 3 ex. (ZMB 29244), north shore, 02°29.75'S, 121°25.81'E, loc. 42-03, on rocks,

coll. K. & T. von Rintelen, 17 Sep.2003; 10 ex. (MZB Cru 1771, n=5; ZMB 29168, n=5), north shore, 02°26.274'S, 121°18.83'E, loc. 133-04, on rocks, coll. K. & T. von Rintelen, 22 Jul.2004; 15 ex. (MZB Cru 1772, n=7; ZMB 29223, n=6), north shore, 02°27.311'S, 121°21.047'E, loc. 09-05, on rocks in shallow water, coll. K. & T. von Rintelen, 7 Jan.2005; 2 ex. (ZMB 29241), north shore, 02°25.67'S, 121°16.54'E, loc. 65-03, on mixed substrate, coll. K. & T. von Rintelen, 25 Sep.2003; 1 ex. (ZMB 29447), south shore, 02°27.84'S, 121°13.88'E, loc. 63-03, on rocks, coll. K. & T. von Rintelen, 24 Sep.2003; 1 ex. (MZB Cru 1773), south shore, at small islands, 02°28.476'S, 121°15.64'E, loc. 138-04, on rocks, coll. K. & T. von Rintelen, 24 Jul.2004; 2 ex. (MZB Cru 1774), north shore, 02°27.418'S, 121°21.533'E, loc. 10-05, on mixed substrate, coll. K. & T. von Rintelen, 7 Jan.2005; 1 ex. (MZB Cru 1775), south shore, canal between island and mainland, 02°28.46'S, 121°15.83'E, loc. 62-03, on rocks, coll. K. & T. von Rintelen, 1 Oct.2003; 1

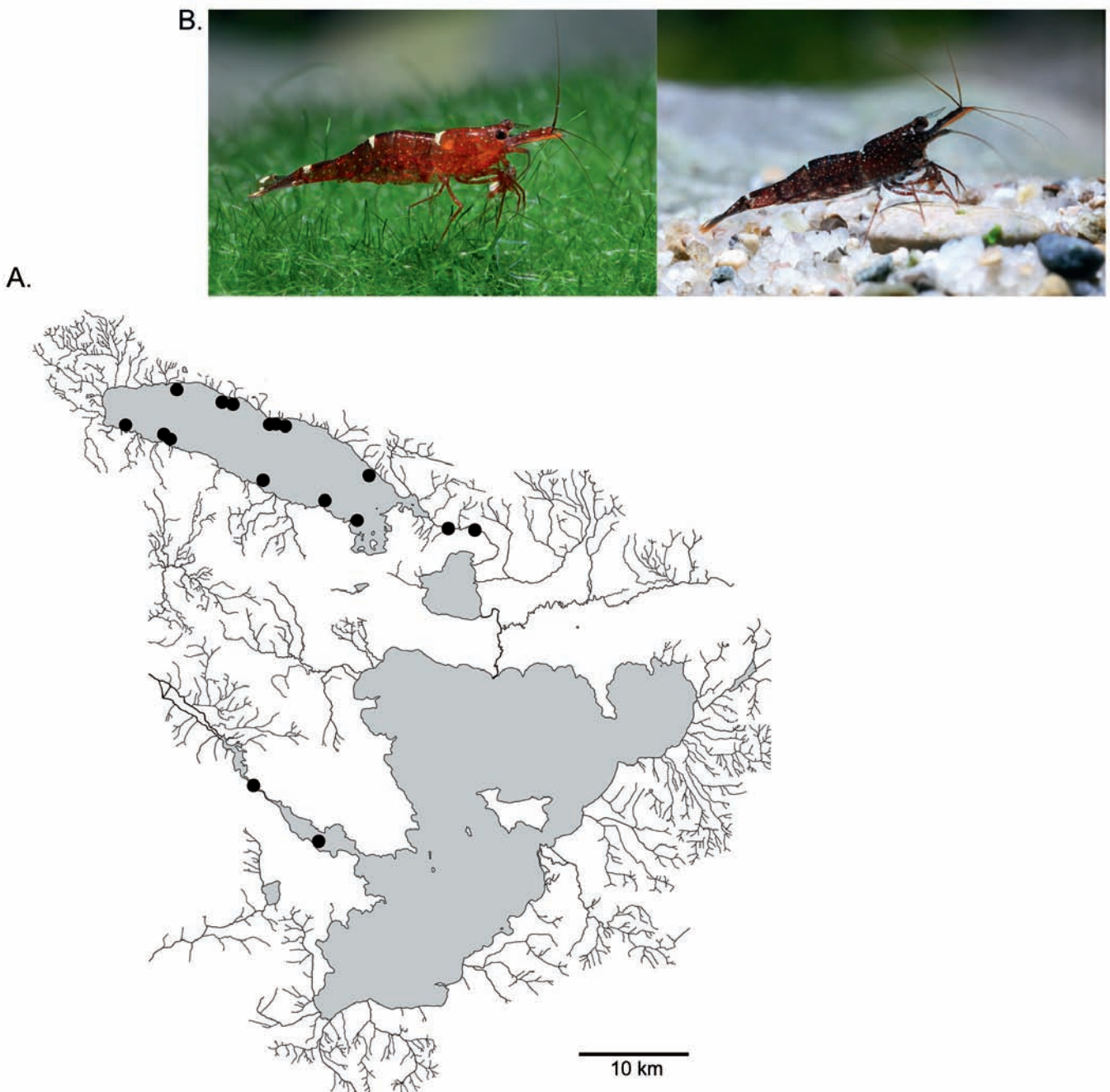


Fig. 18. *Caridina loehae* from the Malili lake system. A. Distribution. B. Colour pattern of living animals (not to scale). Pictures courtesy of Chris Lukhaup.

Table 8. Summary of standard morphometric parameters for *Caridina loehae*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	2.2-2.9	2.6 $\pm$ 0.2	2.6	27
rl / cl	0.5-1.3	0.8 $\pm$ 0.1	0.8	29
n dorsal rostral teeth	14-20	17 $\pm$ 2	17	29
n ventral rostral teeth	1-8	4 $\pm$ 2	4	29
abds6 / cl	0.5-0.8	0.6 $\pm$ 0.0	0.7	27
abds6 / abds5	1.5-2.1	1.8 $\pm$ 0.2	1.9	20
abds6 / h tel	0.9-1.7	1.0 $\pm$ 0.2	1.0	20
h tel / w tel	3.1-3.5	3.3 $\pm$ 0.2	3.3	6
n spines uropodal diaeresis	9-14	12 $\pm$ 2	11	5
h ch1 / w ch1	1.9-2.7	2.1 $\pm$ 0.2	2.1	27
h ch1 / h ca1	0.9-1.8	1.1 $\pm$ 0.2	1.0	30
h ca1 / w ca1	2.5-4.7	3.2 $\pm$ 0.5	3.3	26
h ch2 / w ch2	2.3-3.1	2.7 $\pm$ 0.2	2.6	26
h ch2 / h ca2	0.6-1.0	0.7 $\pm$ 0.1	0.6	30
h ca2 / w ca2	5.4-8.1	6.7 $\pm$ 0.7	6.7	27
n spines p3	2-6	3 $\pm$ 2	3	5
n spines p5	12-16	15 $\pm$ 2	16	5

ex. (MZB Cru 1776), south shore, 02°27.85'S, 121°13.87'E, loc. 125-04, on rocks, coll. P. Koller & K. von Rintelen, 1 Aug.2004; 36 ex. (MZB Cru 1780, n=14; ZMB 29084, n=22), Petea River, 02°32.64'S, 121°29.51'E, loc. 101-03, on rocks, coll. K. & T. von Rintelen, 6 Oct.2003; 27 ex. (MZB Cru 1781, n=13; ZMB 29460, n=14), 02°32.672'S, 121°30.137'E, loc. F4-04, substrate unknown, coll. F. Herder, 25 Mar.2004.

Lake Towuti – 1 ex. (MZB Cru 17771), outlet bay, at Cape Kombe, 02°48.083'S, 121°23.049'E, loc. 118-04, on mixed substrate, coll. K. & T. von Rintelen, 29 Jul.2004; 8 ex. (MZB Cru 1779), Larona River, close to outlet bay, 02°45.06'S, 121°20.12'E, loc. 50-03, on rocks, coll. K. & T. von Rintelen, 21 Sep.2003.

**Description.** – Carapace length 2.2-2.9 mm (n=27). Rostrum (Fig. 19A,B; Table 8) short, reaching near or to end of second segment of antennular peduncle, 0.5-1.3 times as long as carapace (n=29), armed dorsally with 14-20 teeth (including 3-5 teeth posterior to orbital margin), armed ventrally with 1-8 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.5-0.7 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.8-1.1 times as long as carapace (n=5), second segment 1.6-1.8 times length of third segment, third segment 0.3-0.4 times length of basal segment. Stylocerite reaching 0.9-1.0 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 19D) 3.7-4.7 times as long as wide (n=5).

Sixth abdominal somite 0.5-0.8 times length of carapace (n=27), 1.5-2.1 times as long as fifth somite (n=20), 0.9-1.7 times length of telson (n=20). Telson (Fig. 19F,K) 3.1-3.5 times as long as wide (n=6), distal margin rounded, without projection, with 3-4 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 3-4 pairs of spines, lateral pair distinctly longer than intermediate pairs. Preanal carina (Fig.

19C) rounded, without a spine. Uropodal diaeresis (Fig. 19E) with 9-14 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipods only present on first two pereopods. Mouthparts as described by Cai et al. (2009).

Chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig. 19N-P); chela of first pereopod 1.9-2.7 times as long as wide (n=27), 0.9-1.8 times length of carpus (n=30); tips of fingers rounded, without hooks; dactylus 1.4-1.6 times as long as palm (n=6); carpus 2.5-4.7 times as long as wide (n=26), 1.2-1.3 times length of merus (n=5). Chela of second pereopod 2.3-3.1 times as long as wide (n=26), 0.6-1.0 times length of carpus (n=30); tips of fingers rounded, without hooks, dactylus 1.6-2.1 times as long as palm (n=6); carpus 5.4-8.1 times as long as wide (n=27), 1.3-1.5 times as long as merus (n=6).

Third pereopod (Fig. 19G,H) slender, dactylus 2.7-3.6 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 2-6 accessory spines on flexor margin; propodus 10.2-17.2 times as long as wide, 3.7-7.3 times as long as dactylus; carpus 4.6-6.1 times as long as wide, 0.6-0.7 times as long as propodus, 0.5-0.7 times as long as merus; merus 6.8-9.6 times as long as wide, bearing 1-4 strong, movable spines on posterior margin of outer surface.

Fifth pereopod slender (Fig. 19I,J), dactylus 3.2-4.0 times as long as wide (terminal spine included, without spines of

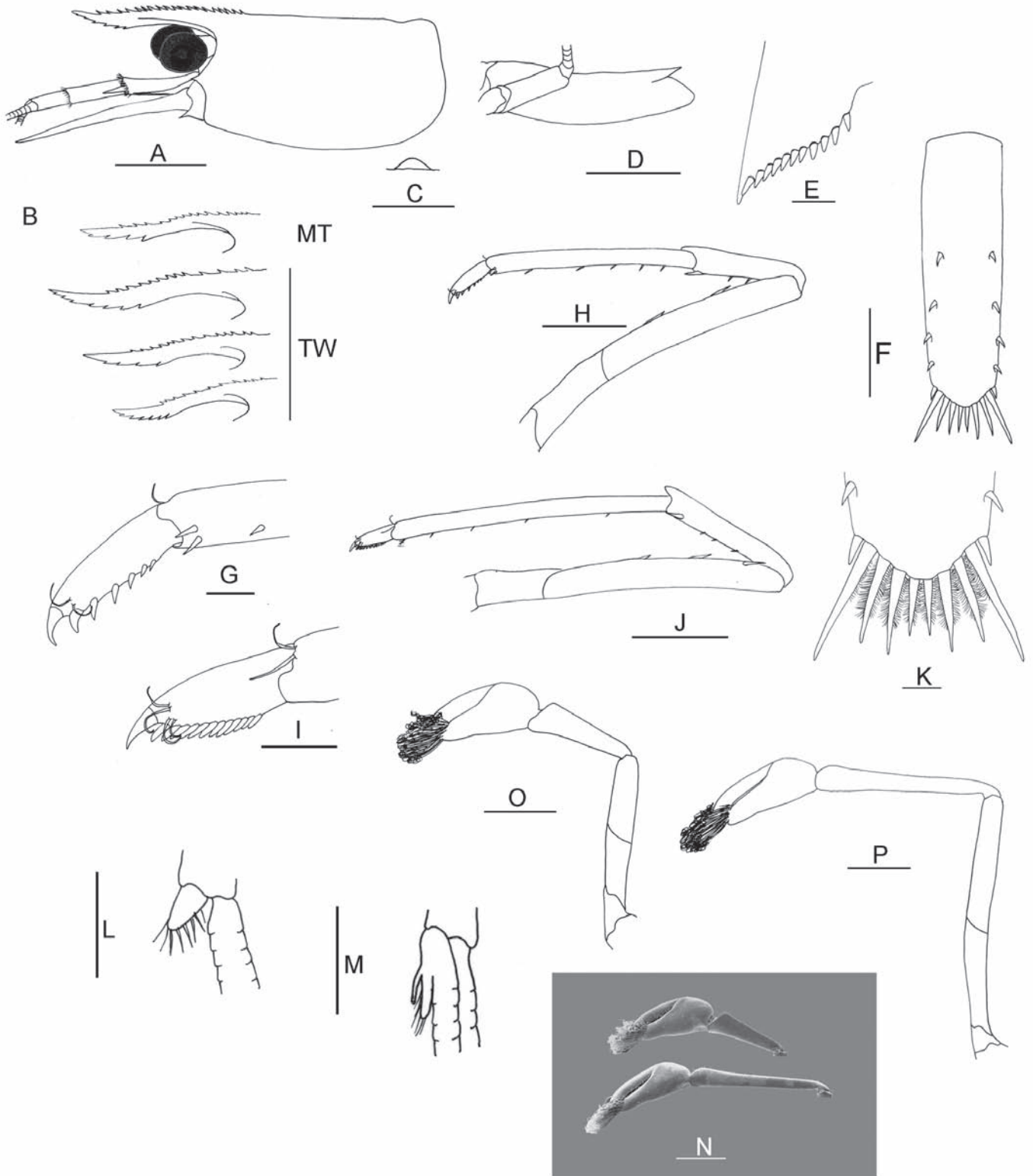


Fig. 19. *Caridina loehae* from the Malili lake system. A. Cephalothorax and cephalic appendages, female (ZMB 29066); B. Woltereck's drawings of the rostrum, from two lakes (modified from 1937a); C. Preanal carina; D. Scaphocerite; E. Uropodal diaeresis; F. Telson, female (ZMB 29080); G. Dactylus of third pereiopod, female (ZMB 29118); H. Third pereiopod; I. Dactylus of fifth pereiopod; J. Fifth pereiopod; K. Distal end of telson, female (ZMB 29080); L. Endopod of male first pleopod (ZMB 29066); M. Appendix masculina of male second pleopod; N. SEM image of chela and carpus of first and second pereiopods, female (ZMB 29233); O. First pereiopod; P. Second pereiopod. Scale bars: A, D = 1.0 mm; C, F, H, J, L-P = 0.5 mm; E, G, I, K = 0.1 mm; B = no scale available.

flexor margin; n=5), terminating in one large claw with 12-16 accessory spines on flexor margin; propodus 12.8-20.3 times as long as wide, 5.2-8.1 times as long as dactylus; carpus 5.8-7.8 times as long as wide, 0.5-0.6 times as long as propodus, 0.5-0.7 times as long as merus; merus 7.9-12.6 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 19L) elongated triangular, 1.8-2.3 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 19M) 0.8-0.9 times length of appendix masculina (n=5).

Ovigerous females with 10-19 eggs (n=4 females); egg size 0.8-1.1 x 0.5-0.7 mm (n=60, eggs with and without eyes).

**Distribution.** – *C. loehae* is endemic to the Malili lake system. There, however, widely distributed in Lake Matano and in Petea River, but was only found in the outlet bay area of Lake Towuti (Fig. 18A). Woltereck mentioned the occurrence of *C. loehae* at three other localities in Lake Towuti, e.g. at Loeha Island, therefore the distribution shown here may not be complete.

**Biology and ecology.** – *C. loehae* is a typical hard substrate dweller, mainly occurring on and under smaller rocks, and on gravel in shallow water (above 5 m), where it is often collected with other rock dwellers such as *C. parvula* and *C. dennerli*. When disturbed, it tries to escape side- or downwards and often stays attached to rocks. The red colour can turn blue in stressed animals.

**Colour pattern.** – Body colouration (including appendages) of *C. loehae* varies from light to dark red with three conspicuous white transversal stripes in regular intervals on the posterior part of the carapace and the abdomen, a scattering of small white spots covering the whole body and uropods with white tips (Fig. 18B), although the white colour is not always strongly pronounced. Eggs were observed to be red.

**Taxonomic remarks.** – Cai et al. (2009: 19) stated: “Specimens of Woltereck (1937a, b) are no longer extant [...]. As all new species described by Woltereck are morphologically close to each other and to stabilize the taxonomic status of those species, neotypes are designated if specimens are available from the recent collections”. Consequently, they designated a neotype for *C. loehae* from Lake Towuti (ovigerous female, cl 2.6 mm, ZRC) (2009: 27).

With regard to its small size (carapace length 2.2-2.9 mm, median 2.6 mm), *C. loehae* is one of the smallest species in the Malili lake system, similar to *C. spongicola* and *C. parvula*. It differs from both by the generally more slender and fragile rostrum, a different rostrum length (reaching near or to end of second segment of antennular peduncle vs. longer in *C. spongicola*), and a lower number of spines on the dactylus of the fifth pereopod (12-16, median 16 vs. 21-31, median 27 in *C. spongicola* and 34-39, median 37 in

*C. parvula*). With regard to the rostrum, it also resembles *C. masapi*. However, *C. loehae* is generally smaller (vs. 2.1-4.6 mm, median 3.1 mm in *C. masapi*), has a shorter rostrum (not overreaching end of second segment of antennular peduncle vs. longer in *C. masapi*), and a lower number of spines on the dactylus of the fifth pereopod (vs. 30-44, median 33 in *C. masapi*).

In the molecular phylogeny (Figs. 63-64), *C. loehae* is genetically distinct from all other ancient lake species.

### *Caridina mahalona* Cai, Wowor & Choy, 2009

(Figs. 20–23; Table 9)

*Caridina mahalona* Cai et al., 2009: 29, Figs. 8-9 (type locality: Lake Mahalona at southwest coast).

**Material examined.** – Lake Mahalona catchment: 1 ex. (ZMB 29466, some SEM material), Ponsoa River, 02°32.243'S, 121°31.818'E, loc. F1-02, substrate unknown, coll. F. Herder, 7 Nov.2002.

Lake Matano catchment – 44 ex. (MZB Cru 1835, n=22; ZMB 29069, n=22, some SEM material), Lawa River, near mouth at northwest shore of Lake Matano, 02°25.75'S, 121°13.27'E, loc. 25-03, on leaf litter, coll. K. & T. von Rintelen, 13 Sep.2003; 20 ex. (MZB Cru 1836, n=10; ZMB 29096, n=10), river, near mouth at northwest corner of Lake Matano, 02°25.88'S, 121°13.08'E, loc. 24-03, on mixed substrate, coll. K. & T. von Rintelen, 13 Sep.2003; 5 ex. (ZMB 29295, some SEM material), small stream northwest of Lake Matano, 02°25.846'S, 121°13.097'E, loc. 126-04, on macrophytes, coll. T. von Rintelen, 1 Aug.2004.

Lake Towuti catchment – 19 ex. (MZB Cru 1840, n=9; ZMB 29067, n=10, some SEM material), Lengkona River, 02°40.82'S, 121°41.77'E, loc. 86-03, on leaf litter, coll. K. & T. von Rintelen, 2 Oct.2003; 1 ex. (ZMB 29192), Kondube River, at road north of Matampi, near Timampu, 02°38.36'S, 121°24.98'E, loc. 37-03, on roots, coll. K. & T. von Rintelen, 15 Sep.2003; 36 ex. (MZB Cru 1841, n=18; ZMB 29210, n=18, some SEM material), Bombongan River, 02°52.38'S, 121°22.54'E, loc. 49-03, on leaf litter, coll. K. & T. von Rintelen, 20 Sep.2003; 17 ex. (MZB Cru 1842, n=9; ZMB 29212, n=8), stream, tributary of Bombongan River, 02°51.59'S, 121°21.61'E, loc. 48-03, on leaf litter, coll. K. & T. von Rintelen, 20 Sep.2003.

Patingko River (Malili lake system) – 35 ex. (MZB Cru 1838, n=17; ZMB 29085, n=18, some SEM material), at road Tabarano, off road Malili-Soroako north of Balambano, 02°38.222'S, 121°14.56'E, loc. 14-03, on mixed substrate, coll. K. & T. von Rintelen, 15 Sep.2003; 1 ex. (ZMB 29184, n=1), Kondara River (tributary of Patingko River), at road Malili-Soroako, east of Leduledu, 02°35.11'S, 121°17.34'E, loc. 36-03, on leaf litter, coll. K. & T. von Rintelen, 15 Sep.2003; 14 ex. (MZB Cru 1839, n=7; ZMB 29196, n=7), south of road Malili-Soroako, 02°37.17'S, 121°14.95'E, loc. 33-03, on rocks, coll. K. & T. von Rintelen, 15 Sep.2003; 14 ex. (ZMB 29197, some SEM material), at road Malili-Soroako, in Togo village, 02°36.53'S, 121°15.56'E, loc. 34-03, on leaf litter, coll. K. & T. von Rintelen, 15 Sep.2003.

Tomori (north of the Malili lake system) – 10 ex. (MZB Cru 1837, n=5; ZMB 29061, n=5, some SEM material), Momonsi River; at road Nuha-Beteleme, 02°25.36'S, 121°21.43'E, loc. 64-03, on leaf litter, coll. K. & T. von Rintelen, 25 Sep.2003.

**Description.** – Carapace length 2.8-5.2 mm (n=17). Rostrum (Fig. 21A-E; Table 9) length variable, short to long, sometimes reaching slightly beyond end of scaphocerite, sometimes distinctly shorter, 0.5-1.0 times as long as carapace (n=21), armed dorsally with 7-21 teeth (including 1-6 teeth posterior to orbital margin), approx. anterior 1/4 to 2/3 unarmed, without subapical teeth armed ventrally with 2-9 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.6-0.7 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.7-0.9 times as long as carapace (n=5), second segment 1.5-1.8 times

length of third segment, third segment 0.3-0.4 times length of basal segment. Stylocerite reaching 0.9-1.0 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 21F,K,P) 3.5-4.1 times as long as wide (n=5).

Sixth abdominal somite 0.5-0.7 times length of carapace (n=17), 1.7-1.9 times as long as fifth somite (n=5), 0.9-1.0 times length of telson (n=17). Telson (Fig. 21G,J,L,O,Q,T) 2.9-3.3 times as long as wide (n=6), distal margin rounded, without projection, with 3-4 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 3-4 pairs of spines, lateral pair distinctly stronger but not always longer than

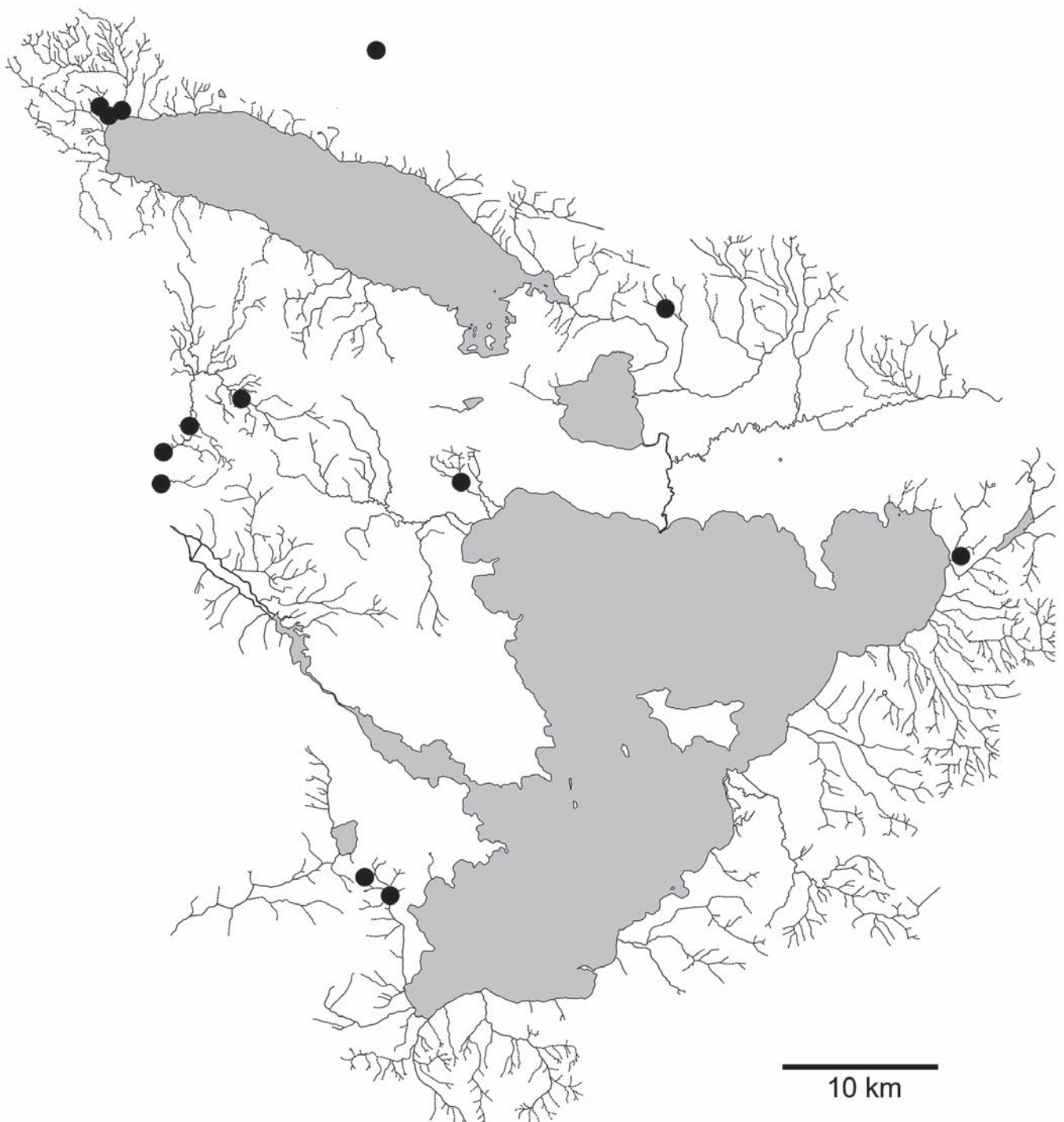


Fig. 20. Distribution of *Caridina mahalona* in the Malili lake system and the Tomori area.



Table 9. Summary of standard morphometric parameters for *Caridina mahalona*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	2.8-5.2	4.5 $\pm$ 0.7	4.4	17
rl / cl	0.5-1.0	0.7 $\pm$ 0.2	0.7	21
n dorsal rostral teeth	7-21	13 $\pm$ 3	14	20
n ventral rostral teeth	2-9	5 $\pm$ 2	4	20
abds6 / cl	0.5-0.7	0.6 $\pm$ 0.0	0.6	17
abds6 / abds5	1.7-1.9	1.8 $\pm$ 0.1	1.8	5
abds6 / h tel	0.9-1.0	0.9 $\pm$ 0.1	0.9	17
h tel / w tel	2.9-3.3	3.2 $\pm$ 0.2	3.2	6
n spines uropodal diaeresis	12-15	13 $\pm$ 1	13	6
h ch1 / w ch1	2.0-2.5	2.3 $\pm$ 0.2	2.4	9
h ch1 / h ca1	0.7-1.4	1.2 $\pm$ 0.1	1.2	24
h ca1 / w ca1	2.5-3.3	2.9 $\pm$ 0.3	2.8	9
h ch2 / w ch2	2.6-3.4	2.9 $\pm$ 0.2	2.8	9
h ch2 / h ca2	0.7-1.3	0.8 $\pm$ 0.1	0.7	23
h ca2 / w ca2	5.6-7.0	6.3 $\pm$ 0.5	6.2	9
n spines p3	5-6	5 $\pm$ 1	5	6
n spines p5	39-57	51 $\pm$ 6	52	6

intermediate pairs. Preanal carina (Fig. 21H,M,R) with a spine. Uropodal diaeresis (Fig. 21I,N,S) with 12-15 movable spinules (n=6).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipod present on first pereopod. Incisor process of mandible (Fig. 23A) ending in a row of 4-5 small teeth, molar process truncated. Lower lacinia of maxillula (Fig. 23B) broadly rounded, upper lacinia elongate, with numerous distinct teeth and setae on inner margin, palp slender. Upper endites of maxilla (Fig. 23C) subdivided, palp short, scaphognathite tapering posteriorly with numerous long, curved setae at posterior end. Distal end of palp of first maxilliped (Fig. 23D) triangular, ending with a finger-like projection; flagellum of the exopod very elongated, endopod high, not exceeding the flagellum of exopod in length. Second maxilliped (Fig. 23F) typical. Third maxilliped (Fig. 23E) with ultimate segment distinctly shorter than penultimate segment.

Chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig. 22E-F,M-N,U-V); chela of first pereopod 2.0-2.5 times as long as wide (n=9), 0.7-1.4 times length of carpus (n=24); tips of fingers rounded, without hooks; dactylus 1.1-1.4 times as long as palm (n=9); carpus 2.5-3.3 times as long as wide (n=9), 1.1-1.4 times length of merus (n=8). Chela of second pereopod 2.6-3.4 times as long as wide (n=9), 0.7-1.3 times length of carpus (n=23); tips of fingers rounded, without hooks, dactylus 1.1-1.5 times as long as palm (n=9); carpus 5.6-7.0 times as long as wide (n=9), 1.3-1.5 times as long as merus (n=8).

Third pereopod (Fig. 22A-B,I-J,Q-R) slender, dactylus 3.0-4.4 times as long as wide (terminal spine included, without spines of flexor margin; n=6), terminating in one large claw with 5-6 accessory spines on flexor margin; propodus 9.0-13.0 times as long as wide, 3.6-4.5 times as long as dactylus; carpus 4.9-5.8 times as long as wide, 0.6-0.7 times as long as propodus, 0.5-0.6 times as long as merus; merus 7.1-10.0 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Fifth pereopod slender (Fig. 22C-D,K-L,S-T), dactylus 3.9-5.4 times as long as wide (terminal spine included, without spines of flexor margin; n=6), terminating in one large claw with 39-57 accessory spines on flexor margin; propodus 9.6-14.9 times as long as wide, 2.8-3.7 times as long as dactylus; carpus 4.7-5.7 times as long as wide, 0.5-0.6 times as long as propodus, 0.6-0.7 times as long as merus; merus 6.1-8.5 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 22G,O,W) elongated triangular, 1.7-2.7 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 22H,P,X) 0.7-0.9 times length of appendix masculina (n=5).

Ovigerous females with 10-24 eggs (n=3 females); egg size 1.0-1.2 x 0.6-0.8 mm (n=28, eggs with and without eyes).

**Distribution.** – *C. mahalona* mainly occurs in rivers within the Malili lakes' catchment (Fig. 20), but was also found at one locality north of Lake Matano (Tomori area), outside of the system. Therefore, it is the only non-endemic species occurring in the Malili system.

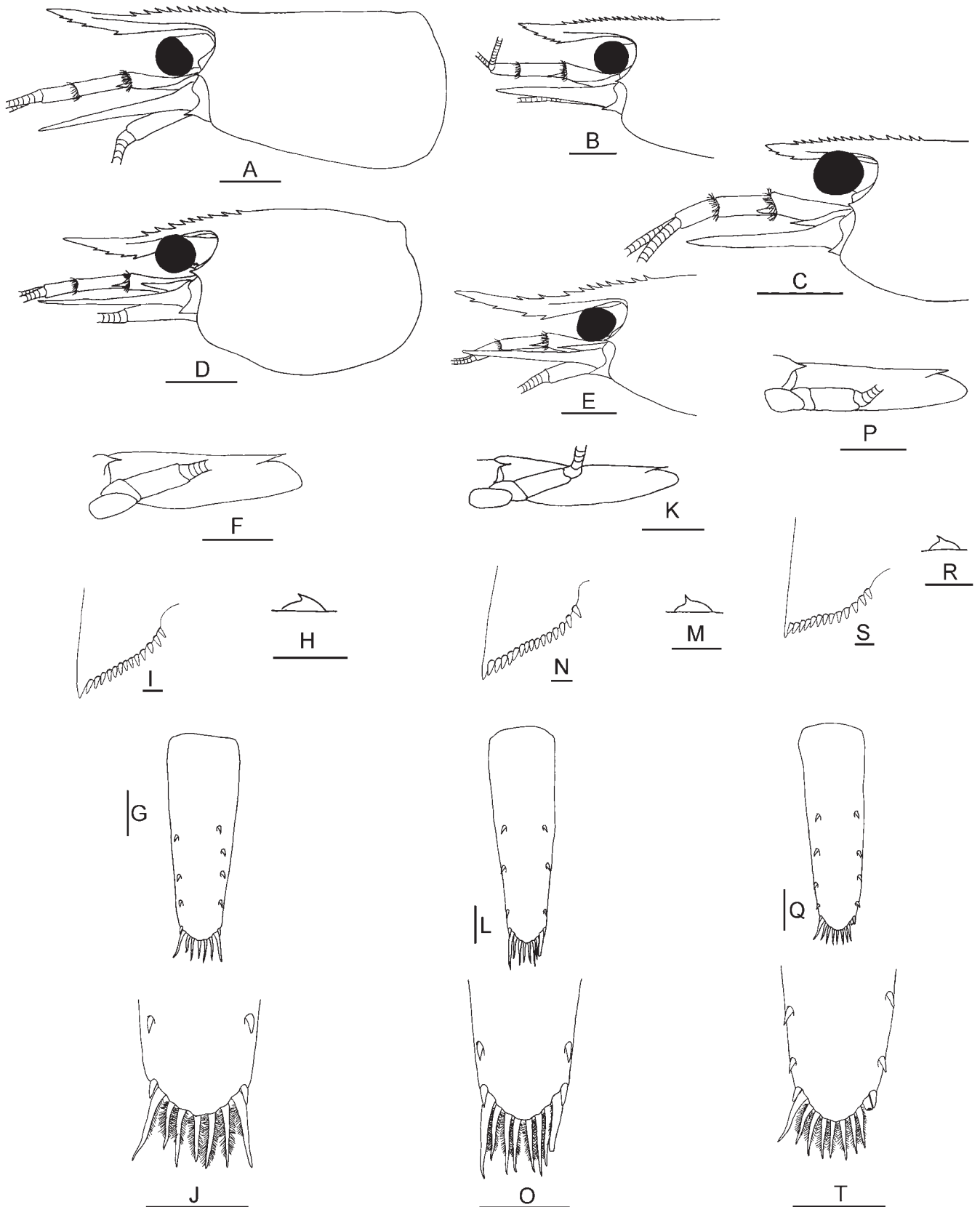


Fig. 21. *Caridina mahalona* from the Malili lake system (each of the three columns shows a representative of a different genetic clade; compare remarks for details). Cephalothorax and cephalic appendages from: A. Male (ZMB 29069); B. Female (ZMB 29061); C. Female (ZMB 29085); D. Male (ZMB 29210); E. Female (ZMB 29067). F. Scaphocerite, female (ZMB 29061); G. Telson, male (ZMB 29069); H. Preanal carina, female (ZMB 29061); I. Uropodal diaeresis, male (ZMB 29069); J. Distal end of telson; K. Scaphocerite, male (ZMB 29085); L. Telson; M. Preanal carina; N. Uropodal diaeresis; O. Distal end of telson; P. Scaphocerite, female (ZMB 29085); Q. Telson, female (ZMB 29197); R. Preanal carina, female (ZMB 29085); S. Uropodal diaeresis, female (ZMB 29197); T. Distal end of telson, female (ZMB 29197). Scale bars: A-F, J, O = 1.0 mm; G-H, J, L-M, O, Q-R, T = 0.5 mm; I, N, S = 0.1 mm.

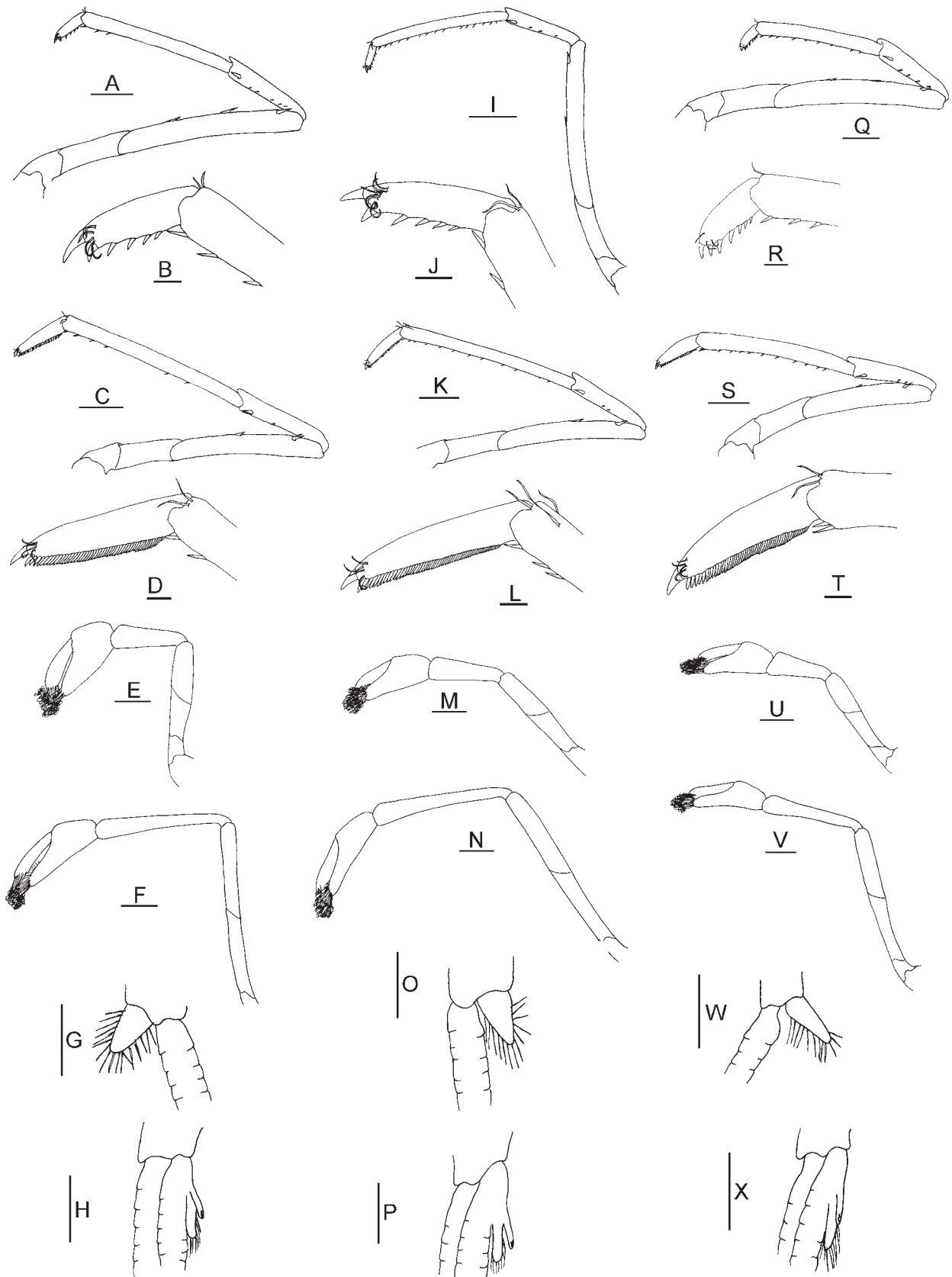


Fig. 22. *Caridina mahalona* from the Malili lake system (each of the three columns shows a representative of a different genetic clade; compare remarks for details). A. Third pereiopod, female (ZMB 29069); B. Dactylus of third pereiopod; C. Fifth pereiopod; D. Dactylus of fifth pereiopod; E. First pereiopod, female (ZMB 29295), F. Second pereiopod; G. Endopod of male first pleopod (ZMB 29061); H. Appendix masculina of male second pleopod; I. Third pereiopod, male (ZMB 29210); J. Dactylus of third pereiopod; K. Fifth pereiopod; L. Dactylus of fifth pereiopod; M. First pereiopod; N. Second pereiopod; O. Endopod of male first pleopod; P. Appendix masculina of male second pleopod; Q. Third pereiopod, female (ZMB 29197); R. Dactylus of third pereiopod; S. Fifth pereiopod; T. Dactylus of fifth pereiopod; U. First pereiopod; V. Second pereiopod; W. Endopod of male first pleopod (ZMB 29085); X. Appendix masculina of male second pleopod. Scale bars: A, C, E-I, K, M-Q, S, U-X = 0.5 mm; B, D, J, L, R, T = 0.1 mm.

**Biology and ecology.** – *C. mahalona* is an exclusively riverine species, dwelling on various kinds of substrate (leaf litter, riverine vegetation, roots, dead wood). Except for one riverine locality very close to Lake Matano (loc. 24-03), where it occurred together with *C. holthuisi*, *C. mahalona* was never found in sympatry with any other species (not even the other riverine species of the Malili lake system, *C. masapi*).

**Colour pattern.** – Without any species specific pattern. Body colouration transparently yellowish or brownish, similar to *C. masapi*, *C. acutirostris*, *C. schenkeli*, and many other riverine species from all over Sulawesi. Large (often ovigerous) females usually appear darker than smaller specimens.

**Taxonomic remarks.** – *C. mahalona* mostly resembles *C. masapi*, but both species were never found together at any locality. *C. mahalona* is generally larger than *C. masapi* (carapace length 2.8-5.2, median 4.4 vs. 2.1-4.6, median 3.1 in *C. masapi*), its rostrum displays a higher degree of variability than in *C. masapi*, and differs by the number of teeth on the dactylus of the fifth pereiopod (39-57, median 52 vs. 30-44, median 33 in *C. masapi*). In specimens with a short rostrum, *C. mahalona* can resemble *C. acutirostris* from Lake Poso, although the scaphocerite usually is more slender (3.5-4.1 times as long as wide vs. 3.0-3.6 times as long as wide in *C. acutirostris*); the same applies to the carpus of the first and second pereiopod (2.5-3.3 and 5.6-7.0 times as long as wide vs. 2.0-2.7 and 4.5-5.9 times as long as wide in *C.*

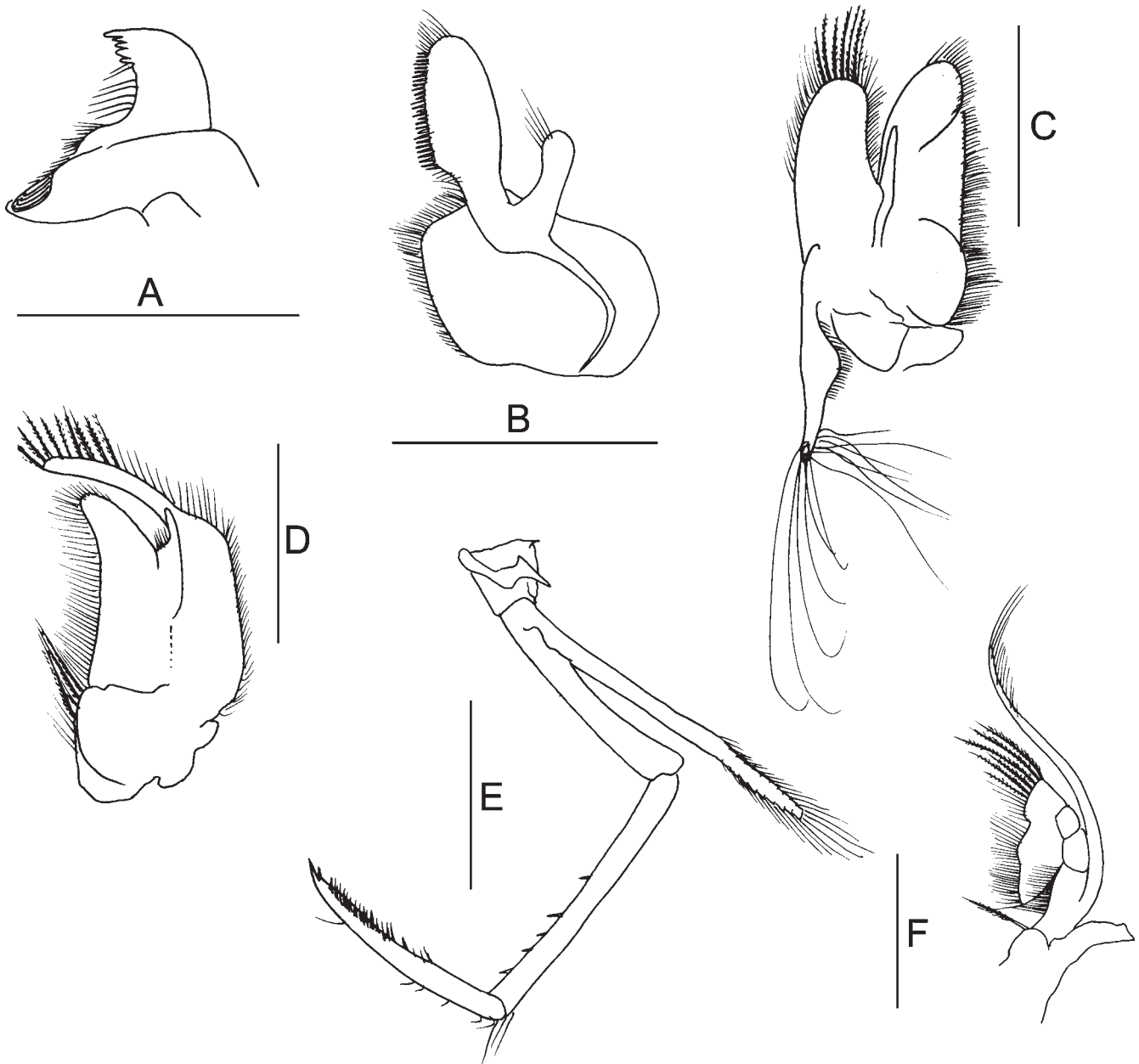


Fig. 23. *Caridina mahalona* from the Malili lake system. A. Mandible (ZMB 29067); B. Maxillula; C. Maxilla; D. first maxilliped; E. third maxilliped; F. second maxilliped. Scale bars: A-F = 1mm.

*acutirostris*). The general range of parameters (for example the number of rostral teeth) is usually higher in *C. mahalona* than in *C. acutirostris* (compare Tables 10,19).

In the molecular phylogeny (Figs. 63-64), *C. mahalona* appears in three allopatric clades (drawings of representatives of each clade are shown in Figs. 21-22). The high degree of rostrum variability partly occurs within populations, and no significant morphological differences were found between members of the different clades. However, the geographic pattern might suggest the existence of cryptic species (compare von Rintelen et al., in review).

### *Caridina masapi* Woltereck, 1937a

(Figs. 24–26; Table 10)

*Caridina Masapi* Woltereck, 1937a: 223, Figs. I.6a-h, pls. 3,6 (type locality: Matanno [Matano] islands, Lake Towuti, Lake Mahalona [Mahalona], Lake Wawontoa [Lontoa], Lake Masapi, small stream between Lake Matano and Lake Mahalona).

*Caridina masapi* – Woltereck, 1937b: 306, fig. 10; Chace, 1997: 16; Fernandez-Leborans et al., 2006b: 1985, Table I; von Rintelen et al., 2008: 2244, Table 1; Cai et al., 2009: 21, Figs. 4-5 (type locality of neotype: southern shore of Lake Masapi).

*Cardina masapi* – Brooks, 1950: 168 (erroneous spelling).

**Material examined.** – Lake Lontoa: 74 ex. (MZB Cru 1689, n=37; ZMB 29038, n=37, some SEM material), southeast shore, 02°40.4'S, 121°43.35'E, loc. 92-03, on mixed substrate, coll. K. & T. von Rintelen, 3 Oct.2003; 16 ex. (MZB Cru 1690, n=8; ZMB 29045, n=8, some SEM material), southwest shore, 02°40.48'S, 121°43.06'E, loc. 93-03, on macrophytes, coll. K. & T. von Rintelen, 3 Oct.2003.

Lake Matano – 13 ex. (MZB Cru 1692), south shore, near cave entrance, 02°29.85'S, 121°18.66'E, loc. 60-03, on mixed substrate, coll. K. & T. von Rintelen, 24 Sep.2003; 5 ex. (ZMB 29083, n=5 and few juveniles), Petea River, approx. 400 m east of Lake Mahalona, 02°34.41'S, 121°30.63'E, loc. 54-03, on mixed substrate, coll. K. & T. von Rintelen, 23 Sep.2003; 27 ex. (MZB Cru 1702, n=14; ZMB 29276, n=13), Petea River, approx. 1.8 km north of Lake Mahalona, 02°34.15'S, 121°31.4'E, loc. F2-04, substrate unknown, coll. F. Herder, 31 Mar.2004; 9 ex. (MZB Cru 1703, n=4; ZMB 29280, n=5), Petea River, 02°34.17'S, 121°31.21'E, loc. F3-04, substrate unknown, coll. F. Herder, 31 Mar.2004.

Lake Masapi – 170 ex. (MZB Cru 1693, n=70; ZMB 29035, n=100, some SEM material), south shore, 02°50.84'S, 121°21.09'E, loc. 47-03, on mixed substrate, coll. K. & T. von Rintelen, 20 Sep.2003; 81 ex. (MZB Cru 1694, n=62; ZMB 29277, n=19, some SEM material), south shore, 02°50.837'S, 121°21.116'E, loc. F5-04, on mixed substrate, coll. F. Herder, 15 Apr.2004.

Lake Towuti – 1 ex. (ZMB 29031, n=1 and some juveniles), east shore, 02°40.84'S, 121°41.32'E, loc. 87-03, on *Ottelia*, coll. K. & T. von Rintelen, 2 Oct.2003; 14 ex. (MZB Cru 1695, n=7; ZMB 29046, n=7, some SEM material), north shore, at cape, 02°39.38'S, 121°29.73'E, loc. 67-03, on rocks in shallow water, coll. K. & T. von Rintelen, 26 Sep.2003; 1 ex. (ZMB 29117), west shore, south of Cape Timbalo, 02°42.91'S, 121°26.78'E, loc. 94-03, on rocks in shallow water, coll. K. & T. von Rintelen, 3 Mar.2003; 2 ex. (ZMB 29281), west shore, west of Cape Timbalo, 02°42.631'S, 121°26.389'E, loc. 145-04, on mixed substrate, coll. K. & T. von Rintelen, 26 Jul.2004; 2 ex. (ZMB 29284), northwest shore,

02°40.647'S, 121°24.915'E, loc. 142-04, on leaf litter, coll. K. & T. von Rintelen, 25 Jul.2004; 7 ex. (ZMB 29285), west shore, Cape Bakara, 02°40.771'S, 121°26.11'E, loc. 144-04, on mixed substrate, coll. K. & T. von Rintelen, 26 Jul.2004; 3 ex. (MZB Cru 1696), west shore, at entrance to outlet bay, Cape Larona, 02°48.43'S, 121°24.75'E, loc. 73-03, on leaf litter, coll. K. & T. von Rintelen, 27 Sep.2003; 1 ex. (MZB Cru 1697), southwest shore, Cape Sioloya, 02°50.7'S, 121°26.32'E, loc. 77-03, on leaf litter, coll. K. & T. von Rintelen, 28 Sep.2003; 39 ex. (MZB Cru 1699, n=39), Larona River, close to outlet bay of Lake Towuti, 02°45.8'S, 121°20.8'E, loc. 51-03, on macrophytes, coll. K. & T. von Rintelen, 21 Sep.2003; 54 ex. (MZB Cru 1701, n=27; ZMB 29195, n=27), Towuti catchment, stream at road Wawondula-Timampu, 02°38.47'S, 121°22.76'E, loc. 39-03, on mixed substrate, coll. K. & T. von Rintelen, 16 Sep.2003; 4 ex. (ZMB 29448), Lemolemo River, 02°42.62'S, 121°40.99'E, loc. 85-03, on leaf litter, coll. K. & T. von Rintelen, 2 Oct.2003.

Lampesue River (Malili lake system) – 44 ex. (MZB Cru 1698, n=22; ZMB 29047, n=22), 02°35.4'S, 121°39.85'E, loc. 79-03, on leaf litter, coll. K. & T. von Rintelen, 29 Sep.2003.

Tominanga River (Lake Mahalona) – 3 ex. (ZMB 29072), approx. 1.5 km east of Lake Mahalona, 02°38.73'S, 121°31.95'E, loc. 59-03, on leaf litter, coll. K. & T. von Rintelen, 23 Sep.2003; 3 ex. (ZMB 29209), approx. 2.2 km north of Lake Towuti, 02°36.5'S, 121°31.78'E, loc. 58-03, on leaf litter, coll. K. & T. von Rintelen, 23 Sep.2003.

**Description.** – Carapace length 2.1-4.6 mm (n=56). Rostrum (Fig. 25A-C, Table 10) shorter than antennular peduncle to slightly reaching beyond end of scaphocerite, 0.6-1.3 times as long as carapace (n=56), armed dorsally with 7-21 teeth (including 2-5 teeth posterior to orbital margin), approx. anterior third unarmed or with few teeth widely spaced, armed ventrally with 3-10 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.6-0.7 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.8-1.0 times as long as carapace (n=5), second segment 1.7-2.4 times length of third segment, third segment 0.3 times length of basal segment. Stylocerite reaching 0.9-1.0 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 25E) 3.2-4.5 times as long as wide (n=5).

Sixth abdominal somite 0.4-0.7 times length of carapace (n=56), 1.4-2.1 times as long as fifth somite (n=21), 0.8-1.1 times length of telson (n=37). Telson (Fig. 25I,L) 2.9-3.6 times as long as wide (n=6), distal margin rounded, without projection, with 3-5 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 3-5 pairs of spines, sometimes with one median spine, lateral pair distinctly longer than intermediate spines, median spine or pair of spines usually shortest. Preanal carina (Fig. 25D) with a spine. Uropodal diaeresis (Fig. 25F) with 10-14 movable spinules (n=6).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipod present on first pereopod. Incisor process of mandible (Fig. 26A) ending in a row of 7-8 small

teeth, molar process truncated. Lower lacinia of maxillula (Fig. 26B) broadly rounded, upper lacinia elongate, with numerous distinct teeth and setae on inner margin, palp slender. Upper endites of maxilla (Fig. 26C) subdivided, palp slender, short, scaphognathite tapering posteriorly with numerous long, curved setae at posterior end. Distal end of palp of first maxilliped (Fig. 26F) triangular, with a finger-like projection; flagellum of the exopod very stout, endopod high, but not exceed the flagellum of exopod in length. Second maxilliped (Fig. 26E) typical. Third maxilliped (Fig. 26D) with ultimate segment as long as penultimate segment.

Chela and carpus of first pereiopod distinctly stouter and broader than chela and carpus of second pereiopod (Fig. 25M-O); chela of first pereiopod 1.9-2.9 times as long as wide (n=25), 0.9-1.3 times length of carpus (n=56); tips of fingers rounded, without hooks; dactylus 1.1-1.3 times as long as palm (n=12); carpus 2.1-4.6 times as long as wide (n=25), 1.1-1.3 times length of merus (n=5). Chela of second pereiopod 2.4-3.9 times as long as wide (n=25), 0.6-1.6 times length of carpus (n=55); tips of fingers rounded, without hooks, dactylus 1.2-1.5 times as long as palm (n=12); carpus 5.0-8.1 times as long as wide (n=25), 1.4-1.6 times as long as merus (n=5).

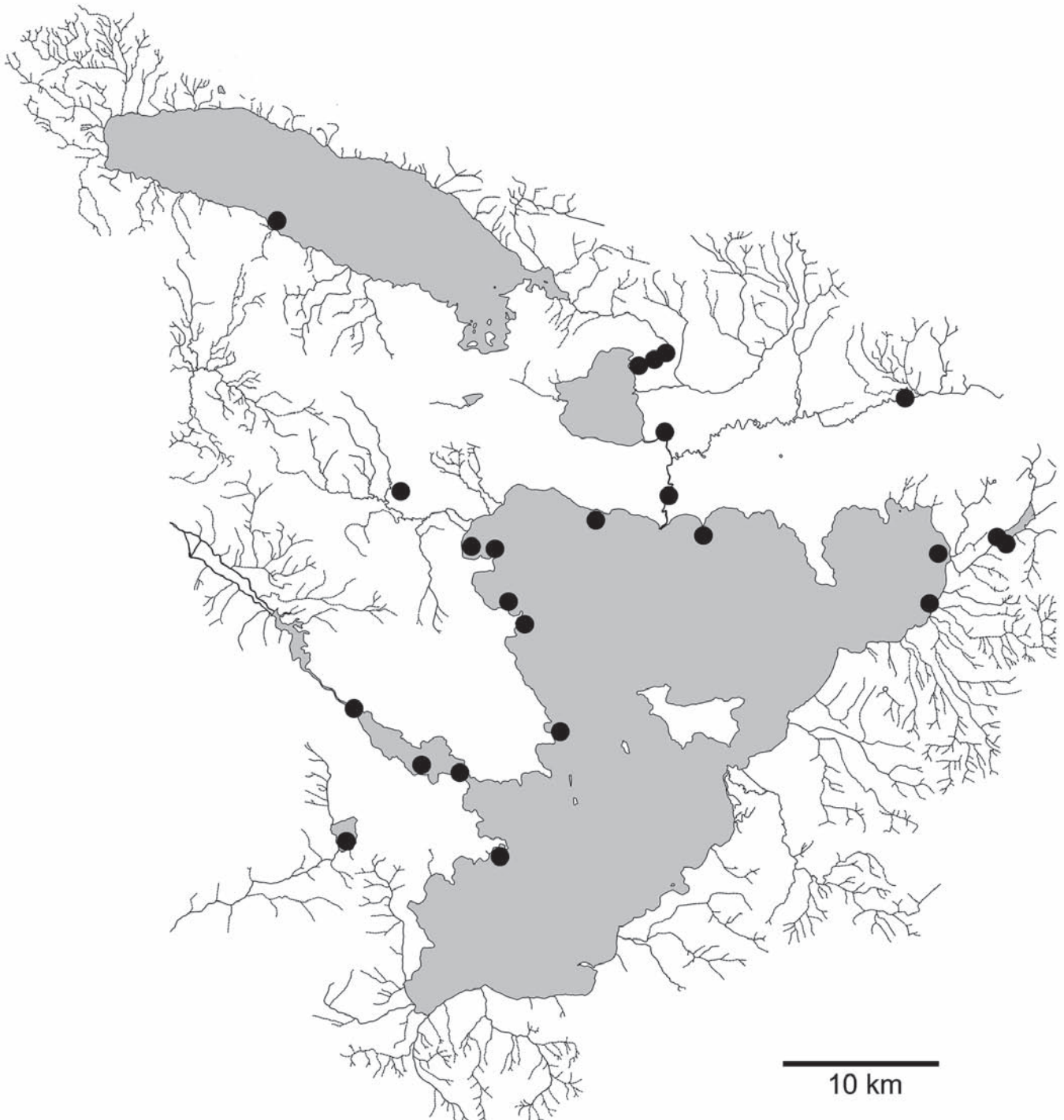


Fig. 24. Distribution of *Caridina masapi* in the Malili lake system.

Table 10. Summary of standard morphometric parameters for *Caridina masapi*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	2.1-4.6	3.1 $\pm$ 0.6	3.1	56
rl / cl	0.6-1.3	0.8 $\pm$ 0.1	0.8	56
n dorsal rostral teeth	7-21	13 $\pm$ 2	13	56
n ventral rostral teeth	3-10	6 $\pm$ 2	6	56
abds6 / cl	0.4-0.7	0.6 $\pm$ 0.1	0.6	56
abds6 / abds5	1.4-2.1	1.8 $\pm$ 0.1	1.9	21
abds6 / h tel	0.8-1.1	1.0 $\pm$ 0.1	1.0	37
h tel / w tel	2.9-3.6	3.3 $\pm$ 0.3	3.3	6
n spines uropodal diaeresis	10-14	12 $\pm$ 2	12	6
h ch1 / w ch1	1.9-2.9	2.3 $\pm$ 0.2	2.3	25
h ch1 / h ca1	0.9-1.3	1.2 $\pm$ 0.1	1.2	56
h ca1 / w ca1	2.1-4.6	2.7 $\pm$ 0.6	2.5	25
h ch2 / w ch2	2.4-3.9	3.1 $\pm$ 0.4	3.1	25
h ch2 / h ca2	0.6-1.6	0.7 $\pm$ 0.1	0.7	55
h ca2 / w ca2	5.0-8.1	6.4 $\pm$ 0.9	6.5	25
n spines p3	3-7	6 $\pm$ 2	6	5
n spines p5	30-44	35 $\pm$ 5	33	5

Third pereiopod (Fig. 25G-H) slender, dactylus 3.5-5.9 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 3-7 accessory spines on flexor margin; propodus 12.6-14.8 times as long as wide, 2.9-5.0 times as long as dactylus; carpus 5.4-6.9 times as long as wide, 0.5-0.6 times as long as propodus, 0.5-0.6 times as long as merus; merus 8.1-11.0 times as long as wide, bearing 3-4 strong, movable spines on posterior margin of outer surface.

Fifth pereiopod slender (Fig. 25J-K), dactylus 5.7-7.0 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 30-44 accessory spines on flexor margin; propodus 11.6-15.3 times as long as wide, 2.6-3.3 times as long as dactylus; carpus 5.0-5.9 times as long as wide, 0.5 times as long as propodus, 0.6 times as long as merus; merus 9.0-9.8 times as long as wide, bearing 3 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 25Q) elongated triangular, 2.0-2.7 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 25R) 0.8-0.9 times as long as appendix masculina (n=5).

Ovigerous females with 15-41 eggs (n=3 females); egg size 0.7-1.2 x 0.5-0.7 mm (n=54, eggs with and without eyes).

**Distribution.** – *C. masapi* is endemic to the Malili system, where it is widely distributed in the lakes and rivers (Fig. 24). Although there is only a single collecting site from Lake Matano, and none directly from Lake Mahalona, Woltereck (1937a: 223, b: 306) reports this species from another locality in Lake Matano (“Matanno islands”), which are further west of the current collecting site on the south coast) and Lake

Mahalona. So far, it is the only shrimp species occurring in Lake Masapi and Lake Lontoa.

**Biology and ecology.** – *C. masapi*, similarly to *C. lanceolata*, was found on various kinds of often mixed, but mainly soft substrate (e.g. macrophytes and leaf litter). Thus, it seems rather to be a generalist with a respective feeding strategy (compare von Rintelen et al., in review). The cheliped morphology does not show any conspicuity, unlike in most other species from the Malili lakes (for example the unusually slender pereiopods in *C. lingkonae*, *C. spinata*, and *C. profundicola*).

**Colour pattern.** – Yellowish or brownish to transparent, often with transversal dark or light bands, but without an always equally pronounced pattern. The colouration resembles that of many riverine *Caridina* species from Sulawesi, which are either dark (brownish) or lightly (yellowish-transparent) coloured. Large (often ovigerous) females usually appear darker than smaller specimens.

**Taxonomic remarks.** – Cai et al. (2009: 19) stated: “Specimens of Woltereck (1937a, b) are no longer extant [...]. As all new species described by Woltereck are morphologically close to each other and to stabilize the taxonomic status of those species, neotypes are designated if specimens are available from the recent collections”. Consequently, they designated a neotype for *C. masapi* from Lake Masapi (male, cl 2.9 mm, ZRC) (2009: 21).

Here, *C. masapi* is regarded as a riverine species (that also enters the lakes) rather than a typical lacustrine species, because of its occurrence in all five lakes and the surrounding rivers. *C. lanceolata* is also widely distributed in the lakes (excluding Lake Masapi and Lake Lontoa), but does not occur in any tributary to the lakes. Thus, we here regard it

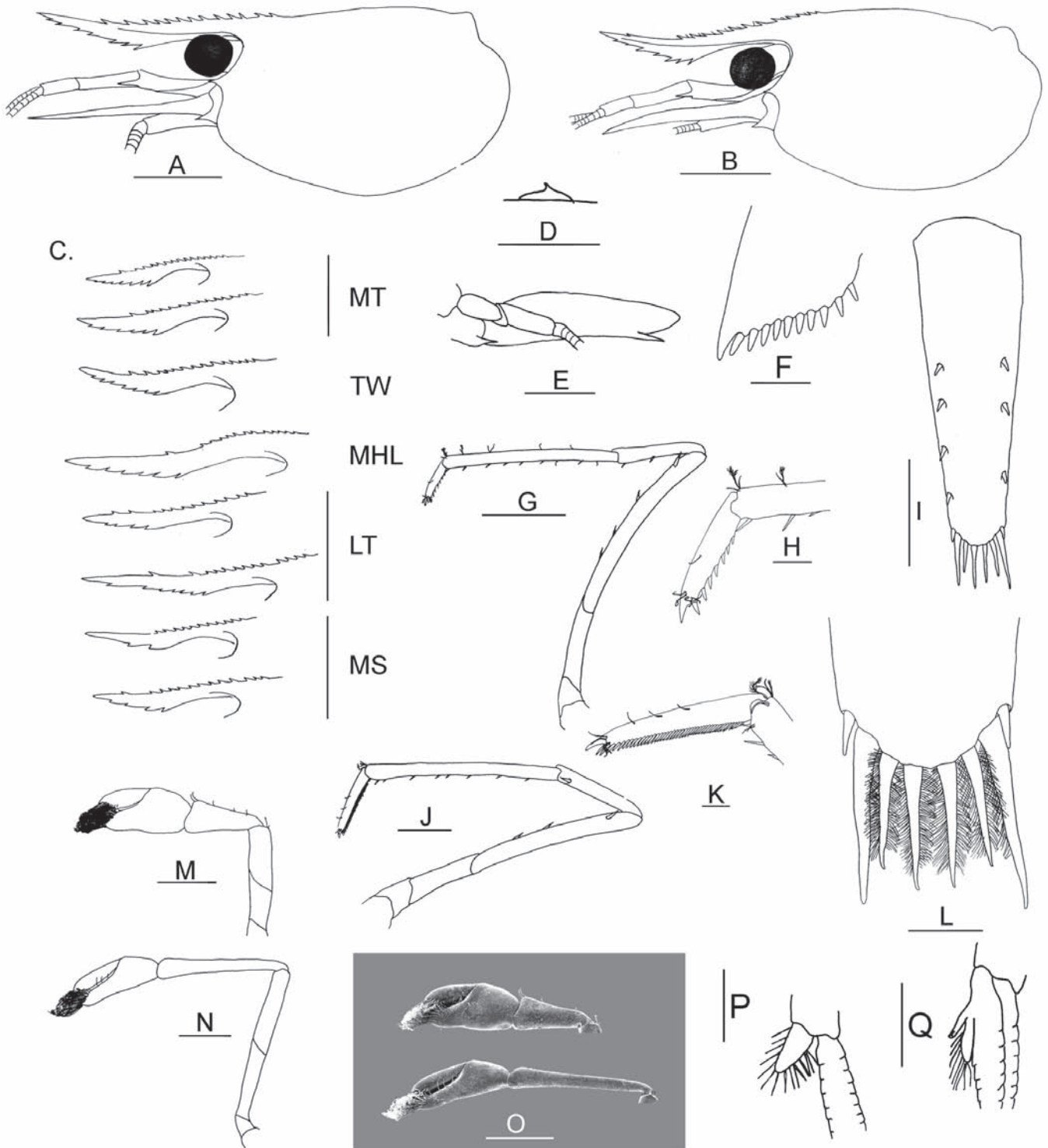


Fig. 25. *Caridina masapi* from the Malili lake system. A. Cephalothorax and cephalic appendages, female (ZMB 29038); B. Cephalothorax and cephalic appendages, male (ZMB 29277); C. Woltereck's drawings of the rostrum, from all Malili lakes (modified from 1937a); D. Preanal carina, female (ZMB 29277); E. Scaphocerite, F. Uropodal diaeresis, male (ZMB 29277); G. third pereiopod, female (ZMB 29277); H. Dactylus of third pereiopod; I. Telson, male (ZMB 29277); J. fifth pereiopod, female (ZMB 29277); K. Dactylus of fifth pereiopod; L. Distal end of telson, male (ZMB 29277); M. First pereiopod; N. Second pereiopod; O. SEM image of chela and carpus of first and second pereiopods; P. Endopod of male first pleopod; Q. Appendix masculina of male second pleopod. Scale bars: A-B, E = 1.0 mm; D, G, I-J, M-Q = 0.5 mm; F, H, K-L = 0.1 mm; C = no scale available.



as a lacustrine species. The rostrum superficially resembles *C. loehae*, but it appears less fragile and longer (usually overreaching end of second segment of antennular peduncle vs. not overreaching in *C. loehae*). Furthermore, both species show a different number of spines on the dactylus of the fifth pereiopod (30-44, median 33 vs. 12-16, median 16 in *C. loehae*). Also, *C. masapi* is similar to *C. mahalona*, the other

riverine species of the Malili lake system, but the rostrum is not as variable as in *C. mahalona* and the anterior dorsal part is not always unarmed. It is generally smaller than *C. mahalona* (carapace length 2.1-4.6 mm, median 3.1 mm vs. 2.8-5.2 mm, median 4.4 mm in *C. mahalona*) and differs by the number of teeth on the dactylus of the fifth pereiopod (vs. 39-57, median 52 in *C. mahalona*). *C. masapi* can

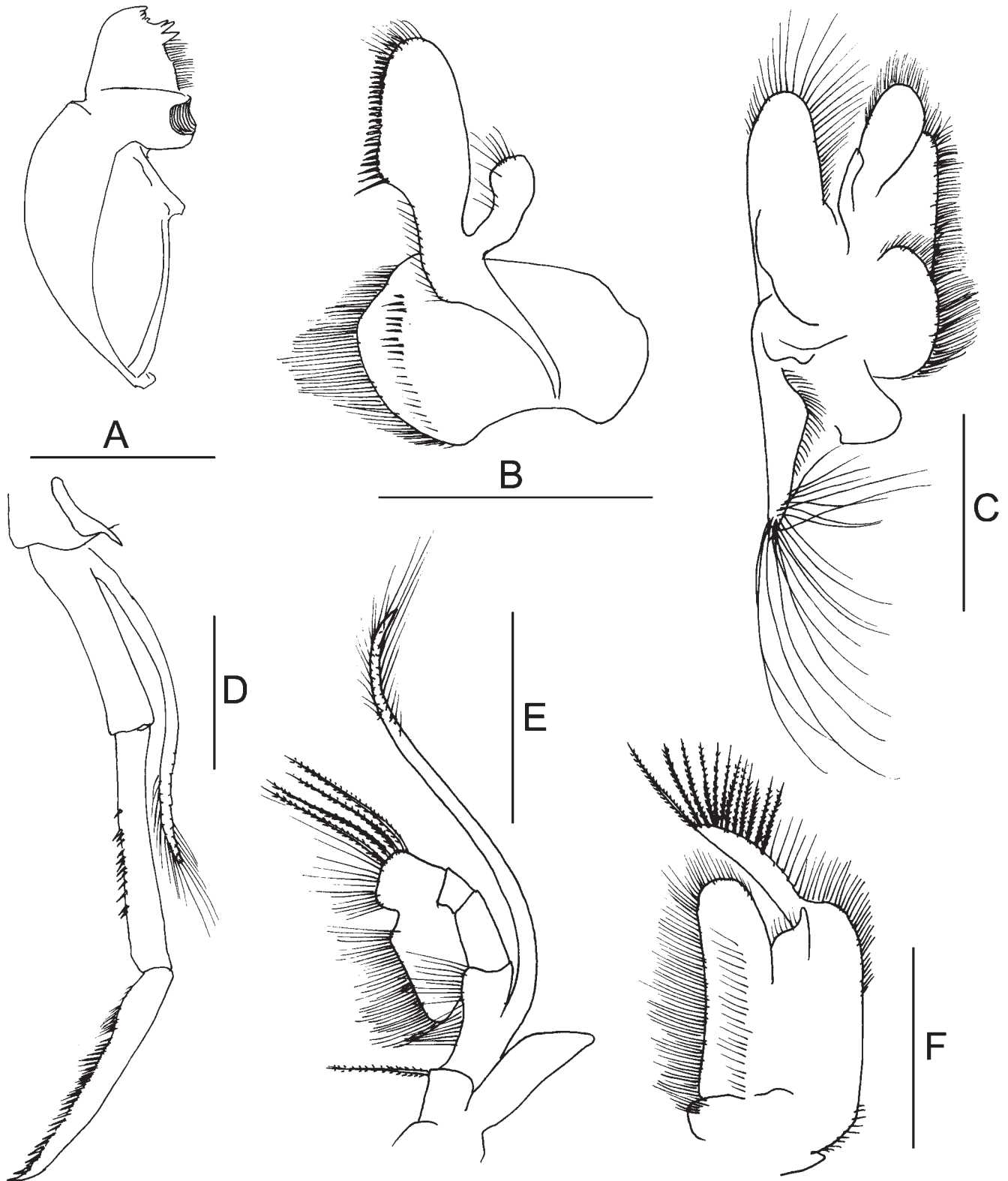


Fig. 26. *Caridina masapi* from the Malili lake system. A. Mandible (ZMB 29277); B. Maxillula; C. Maxilla; D. third maxilliped; E. second maxilliped; F. first maxilliped. Scale bars: A-F = 1mm.

resemble *C. holthuisi*, but the rostrum in *C. masapi* usually differs by a conspicuous unarmed gap on the dorsal margin (sometimes with few teeth widely spaced) and a more slender and cambered shape (vs. usually straight and broader with a more or less thorough denticulation in *C. holthuisi*).

*C. masapi* is genetically distinct from *C. loehae* and *C. mahalona* (Figs. 63-64). *C. masapi* appears in two allopatric clades. One is restricted to Lake Masapi (MS; Fig. 64), the other one to several lakes and rivers. This might hint at the existence of cryptic species (compare von Rintelen et al., in review).

***Caridina parvula*, new species**

(Figs. 27–29; Table 11)

**Material examined.** – Holotype: ovigerous female (cl 3.2 mm)(MZB Cru 2127), Lake Towuti, southwest shore, Cape Sioloya, 02°50.7'S, 121°26.32'E, loc. 77-03, on rocks, coll. K. & T. von Rintelen, 28 Sep.2003.

Paratypes (Lake Matano) – 2 ex. (ZMB 29221), north shore, 02°27.418'S, 121°21.533'E, loc. 10-05, on mixed substrate, coll. K. & T. von Rintelen, 7 Jan.2005; 1 ex. (ZMB 29229), east shore, just south of entrance to outlet bay, 02°31.54'S, 121°27.0'E, loc. 43-03, on rocks in shallow water, coll. K. & T. von Rintelen, 18

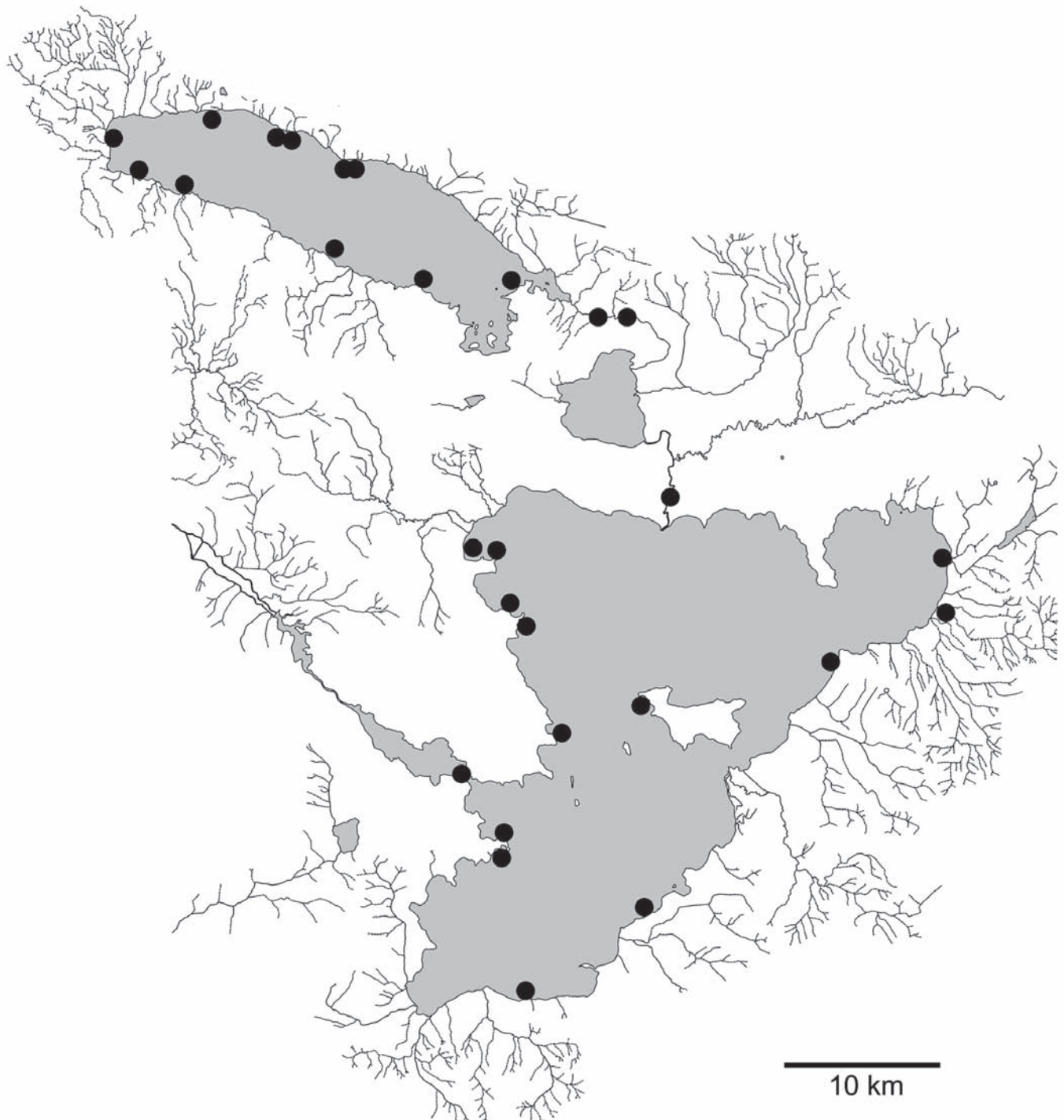


Fig. 27. Distribution of *Caridina parvula* in the Malili lake system.

Table 11. Summary of standard morphometric parameters for *Caridina parvula*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	2.1-3.0	2.6 $\pm$ 0.3	2.6	15
rl / cl	0.4-0.8	0.5 $\pm$ 0.1	0.5	15
n dorsal rostral teeth	11-18	15 $\pm$ 2	14	15
n ventral rostral teeth	2-6	4 $\pm$ 1	4	15
abds6 / cl	0.5-0.6	0.6 $\pm$ 0.0	0.6	14
abds6 / abds5	1.4-1.9	1.6 $\pm$ 0.2	1.6	7
abds6 / h tel	0.9-1.0	0.9 $\pm$ 0.0	0.9	13
h tel / w tel	2.8-3.4	3.1 $\pm$ 0.2	3.1	5
n spines uropodal diaeresis	12-18	16 $\pm$ 2	16	5
h ch1 / w ch1	2.2-2.5	2.4 $\pm$ 0.1	2.4	10
h ch1 / h ca1	0.9-1.6	1.1 $\pm$ 0.2	1.0	14
h ca1 / w ca1	3.3-4.1	3.8 $\pm$ 0.2	3.8	10
h ch2 / w ch2	2.5-3.4	3.1 $\pm$ 0.2	3.1	10
h ch2 / h ca2	0.5-1.2	0.7 $\pm$ 0.2	0.6	14
h ca2 / w ca2	4.3-9.8	7.8 $\pm$ 1.6	8.0	10
n spines p3	2-3	3 $\pm$ 1	3	4
n spines p5	34-39	37 $\pm$ 2	37	4

Sep.2003; 1 ex. (ZMB 29242), north shore, 02°25.67'S, 121°16.54'E, loc. 65-03, on mixed substrate, coll. K. & T. von Rintelen, 25 Sep.2003; 17 ex. (MZB Cru 1801, n=8; ZMB 29243, n=9, some SEM material), west shore, north of Lake Matano, 02°26.91'S, 121°13.01'E, loc. 83-03, on rocks, coll. K. & T. von Rintelen, 1 Oct.2003; 2 ex. (ZMB 29247), south shore, east of Soroako, just west of Cape Patipuoho, 02°31.57'S, 121°23.41'E, loc. 99-03, on rocks, coll. K. & T. von Rintelen, 5 Oct.2003; 2 ex. (MZB Cru 1802), north shore, 02°26.274'S, 121°18.83'E, loc. 133-04, on rocks, coll. K. & T. von Rintelen, 22 Jul.2004; 2 ex. (MZB Cru 1803), south shore, 02°27.85'S, 121°13.87'E, loc. 125-04, on rocks, coll. P. Koller & K. von Rintelen, 1 Aug.2004; 2 ex. (MZB Cru 1805), south shore, Soroako, INCO boat house, 02°30.71'S, 121°20.45'E, loc. 19-03, on rocks, coll. K. & T. von Rintelen, 19 Sep.2003; 3 ex. (MZB Cru 1806), south shore, canal between island and mainland, 02°28.46'S, 121°15.83'E, loc. 62-03, on rocks, coll. K. & T. von Rintelen, 24 Jul.2004; 1 ex. (MZB Cru 1807), north shore, 02°26.36'S, 121°19.03'E, loc. 84-03, on rocks, coll. K. & T. von Rintelen, 1 Oct.2003; 1 ex. (ZMB 29437), Petea River, 02°32.672'S, 121°30.137'E, loc. F4-04, substrate unknown, coll. F. Herder, 25 Mar.2004; 1 ex. (MZB Cru 1813), Petea River, 02°32.64'S, 121°29.51'E, loc. 101-03, on rocks, coll. K. & T. von Rintelen, 6 Oct.2003.

Paratypes (Lake Mahalona) – 3 ex. (MZB Cru 1814), Tominanga River, approx. 1.5 km east of Lake Mahalona, 02°38.73'S, 121°31.95'E, loc. 59-03, on rocks, coll. K. & T. von Rintelen, 23 Sep.2003.

Paratypes (Lake Towuti) – 1 ex. (ZMB 29020), south shore, approx. 2 km east of Cape Mea, 02°55.8'S, 121°26.92'E, loc. 74-03, on rocks, coll. K. & T. von Rintelen, 28 Sep.2003; 7 ex. (ZMB 29064), southwest shore, Cape Sioloya, 02°50.7'S, 121°26.32'E, loc. 77-03, on rocks, coll. K. & T. von Rintelen, 28 Sep.2003; 5 ex. (ZMB 29097), northwest shore, 02°40.647'S, 121°24.915'E, loc. 142-04, on mixed substrate, coll. K. & T. von Rintelen, 25 Jul.2004; 1 ex. (ZMB 29098), west shore, south of Cape Timbalo, 02°42.91'S, 121°26.78'E, loc. 94-03, on rocks in shallow water, coll. K. & T. von Rintelen, 4 Oct.2003; 2 ex. (ZMB 29108, some SEM material), east shore, south of Cape Tomeraka, 02°44.47'S,

121°37.53'E, loc. 70-03, on rocks, coll. K. & T. von Rintelen, 27 Sep.2003; 10 ex. (MZB Cru 1808, n=5; ZMB 29116, n=5), west shore, at entrance to outlet bay, Cape Larona, 02°48.43'S, 121°24.75'E, loc. 73-03, on leaf litter, coll. K. & T. von Rintelen, 27 Sep.2003; 3 ex. (ZMB 29119, some SEM material), Loeha Island, west shore, 02°45.5'S, 121°31.06'E, loc. 95-03, on rocks, coll. K. & T. von Rintelen, 4 Oct.2003; 1 ex. (ZMB 29226), east shore, 02°52.79'S, 121°31.18'E, loc. 72-03, on rocks, coll. K. & T. von Rintelen, 27 Sep.2003; 6 ex. (ZMB 29263, some SEM material), west shore, west of Cape Timbalo, 02°42.631'S, 121°26.389'E, loc. 145-04, on mixed substrate, coll. K. & T. von Rintelen, 26 Jul.2004; 1 ex. (MZB Cru 1809), northeast shore, at Lengkona, 02°40.483'S, 121°41.382'E, loc. 116-04, on mixed substrate, coll. K. & T. von Rintelen, 28 Jul.2004; 1 ex. (MZB Cru 1810, ovigerous female with freshly hatched juveniles), west shore, north of Cape Sioloya, 02°50.389'S, 121°26.026'E, loc. 03-05, on rocks, coll. Y. Cai, K. & T. von Rintelen, 3 Jan.2005; 4 ex. (MZB Cru 1811), west shore, Cape Bakara, 02°40.771'S, 121°26.11'E, loc. 144-04, on mixed substrate, coll. K. & T. von Rintelen, 26 Jul.2004; 4 ex. (MZB Cru 1812), west shore, north of Cape Wasupute, 02°46.9'S, 121°27.94'E, loc. 78-03, on rocks, coll. K. & T. von Rintelen, 28 Sep.2003; Towuti catchment, Lemolemo River, 3 ex. (ZMB 29028, some SEM material), 02°42.62'S, 121°40.99'E, loc. 85-03, on rocks, coll. K. & T. von Rintelen, 2 Oct.2003.

**Description.** – Carapace length 2.1-3.0 mm (n=15). Rostrum (Fig. 28A; Table 11) short, not reaching to end of second segment of antennular peduncle, 0.4-0.8 times as long as carapace (n=15), armed dorsally with 11-18 teeth (including 2-7 teeth posterior to orbital margin), anterior less densely spaced, armed ventrally with 2-6 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.5-0.6 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.7-0.9 times as long as carapace (n=5), second segment 1.5-1.7 times length of third segment, third segment 0.3-0.4 times length of basal segment. Stylocerite reaching 0.9-1.0 times length of basal segment of antennular

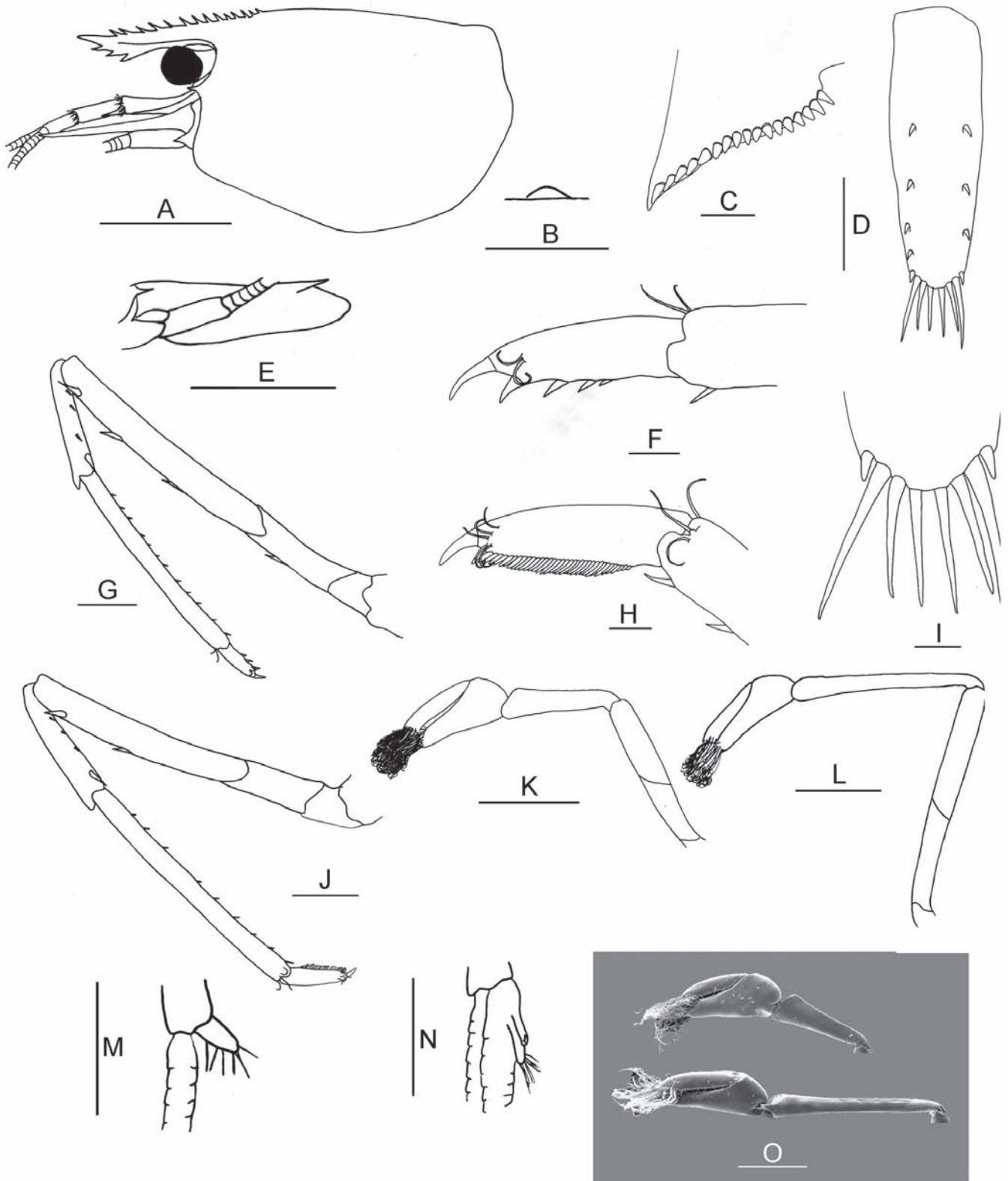


Fig. 28. *Caridina parvula* from the Malili lake system. A. Cephalothorax and cephalic appendages, female (ZMB 29263); B. Preanal carina; C. Uropodal diaeresis, female (ZMB 29028); D. Telson; E. Scaphocerite, F. Dactylus of third pereiopod; G. Third pereiopod; H. Dactylus of fifth pereiopod; I. Distal end of telson; J. Fifth pereiopod; K. First pereiopod, female (ZMB 29243); L. second pereiopod; M. Endopod of male first pleopod (ZMB 29243); N. Appendix masculina of male second pleopod; O. SEM image of chela and carpus of first and second pereiopods, female (ZMB 29119). Scale bars: A, E = 1.0 mm; B, D, G, J-O = 0.5 mm; C, F, H-I = 0.1 mm.

peduncle (n=5). Scaphocerite (Fig. 28E) 3.3-5.4 times as long as wide (n=5).

Sixth abdominal somite 0.5-0.6 times length of carapace (n=14), 1.4-1.9 times as long as fifth somite (n=7), 0.9-1.0 times length of telson (n=13). Telson (Fig. 28D,I) 2.8-3.4 times as long as wide (n=5), distal margin rounded, without projection, with 3-5 pairs of spinules and 1 pair of dorsolateral

spinules; distal end with 3-5 pairs of spines, lateral pair longer than intermediate pairs, median pair usually shortest. Preanal carina (Fig. 28B) rounded, without a spine. Uropodal diaeresis (Fig. 28C) with 12-18 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair

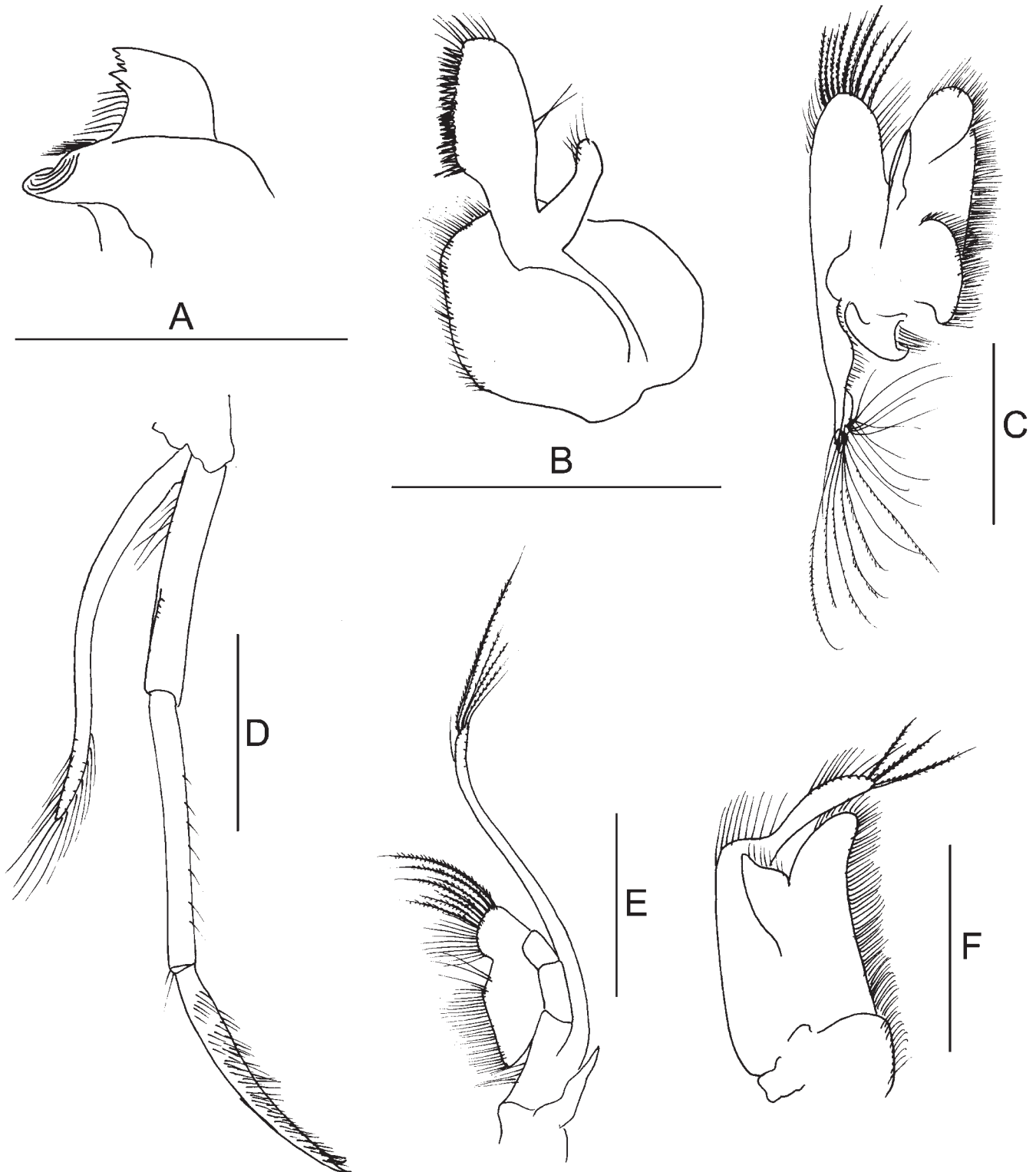


Fig. 29. *Caridina parvula* from the Malili lake system. A. Mandible (ZMB 29064); B. Maxillula; C. Maxilla; D. third maxilliped; E. second maxilliped; F. first maxilliped. Scale bars: A-F = 1mm.

of podobranchs on second maxilliped reduced strongly to a laminate form. Epipod present on first two pereopods. Incisor process of mandible (Fig. 29A) ending in a row of 3-5 small teeth, molar process truncated. Lower lacinia of maxillula (Fig. 29B) broadly rounded, upper lacinia elongate, with numerous distinct teeth and setae on inner margin, palp slender. Upper endites of maxilla (Fig. 29C) subdivided, palp short, scaphognathite tapering posteriorly with numerous long, curved setae at posterior end. Distal end of palp of first maxilliped (Fig. 29F) triangular, not ending with a distinct finger-like projection; flagellum of the exopod stout, endopod high, not exceeding the flagellum of exopod in length. Second maxilliped (Fig. 29E) typical. Third maxilliped (Fig. 29D) with ultimate segment as long as penultimate segment.

First and second pereopod very slender, chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig. 28K-L,O); chela of first pereopod 2.2-2.5 times as long as wide (n=10), 0.9-1.6 times length of carpus (n=14); tips of fingers rounded, without hooks; dactylus 1.4-2.0 times as long as palm (n=5); carpus 3.3-4.1 times as long as wide (n=10), 1.2-1.3 times length of merus (n=5). Chela of second pereopod 2.5-3.4 times as long as wide (n=10), 0.5-1.2 times length of carpus (n=14); tips of fingers rounded, without hooks, dactylus 1.5-1.8 times as long as palm (n=5); carpus 4.3-9.8 times as long as wide (n=10), 1.3-1.4 times as long as merus (n=5).

Third pereopod (Fig. 28F-G) slender, dactylus 3.2-5.0 times as long as wide (terminal spine included, without spines of flexor margin; n=4), terminating in one large claw with 2-3 accessory spines on flexor margin; propodus 8.8-14.3 times as long as wide, 2.8-4.6 times as long as dactylus; carpus 4.8-7.4 times as long as wide, 0.6-0.7 times as long as propodus, 0.5-0.6 times as long as merus; merus 7.2-10.6 times as long as wide, bearing 3-4 strong, movable spines on posterior margin of outer surface.

Fifth pereopod slender (Fig. 28H,J), dactylus 4.0-5.0 times as long as wide (terminal spine included, without spines of flexor margin; n=4), terminating in one large claw with 34-39 accessory spines on flexor margin; propodus 11.3-16.7 times as long as wide, 3.0-4.0 times as long as dactylus; carpus 3.4-6.6 times as long as wide, 0.5-0.6 times as long as propodus, 0.5-0.7 times as long as merus; merus 7.3-10.6 times as long as wide, bearing 1-2 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 28M) elongated triangular, 1.8-2.4 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 28N) 0.8-0.9 times length of appendix masculina (n=5).

Ovigerous females with 12-15 eggs (n=3 females); egg size 0.8-0.9 x 0.5-0.6 mm (n=37, eggs with and without eyes).

**Distribution.** – Endemic to the Malili lake system. There, widely distributed in Lake Matano and Lake Towuti, some

specimens were found in Petea and Tominanga rivers, but none in Lake Mahalona (Fig. 27).

**Biology and ecology.** – This small and rather inconspicuous species often lives in sympatry with other rock dwellers, for example *C. loehae*, under small rocks as its primary substrate in shallow water regions.

**Colour pattern.** – The colour pattern of *C. parvula* is rather inconspicuous compared to other species from the Malili lakes. The body usually shows a light red colouration, which can turn completely blue when under stress, with a few faint white transversal stripes. Body appendages are transparent. Eggs are the same colour as the body.

**Etymology.** – *Caridina parvula* refers to the small size of this new species (the Latin word *parvus* means little).

**Taxonomic remarks.** – *C. parvula* (carapace length 2.1-3.0 mm, median 2.6 mm) is one of the smallest species in the Malili lakes, similarly to *C. loehae* and *C. spongicola*, but differs from *C. spongicola* by a shorter rostrum (not reaching to end of second segment of antennular peduncle vs. longer in *C. spongicola*), by a higher number of spines on the uropodal diaeresis (12-18, median 16 vs. 10-12, median 11 in *C. spongicola*), and by a lower number of spines on the dactylus of the fifth pereopod (34-39, median 37 vs. 21-31, median 27 in *C. spongicola*). The very short and broad rostrum is characteristic for *C. parvula*. The length of the rostrum only resembles *C. loehae*, but is distinctly broader. Both species further differ by a different number of spines on the uropodal diaeresis (vs. 9-14, median 11 in *C. loehae*) and on the dactylus of the fifth pereopod (vs. 12-16, median 16 in *C. loehae*). However, both species often occur in syntopy (on rocks in shallow water) and have a similar colour pattern, although the white markings in *C. loehae* are often more pronounced than in *C. parvula*.

In the molecular phylogeny (Figs. 63-64), *C. parvula* is genetically distinct from all other ancient lake species.

#### *Caridina profundicola*, new species

(Figs. 30-32; Table 12)

**Material examined.** – Holotype: male (cl 3.5 mm) (MZB Cru 1549), Lake Towuti, Loeha Island, southwest shore, 02°45.58'S, 121°31.14'E, loc. 149-04, on boulders in deeper water, coll. K. & T. von Rintelen, 5 Aug. 2004.

Paratypes (Lake Towuti) – 7 ex. (MZB Cru 1552, n=3; ZMB 29025, n=4, some SEM material), east shore, south of Cape Tomeraka, 02°44.47'S, 121°37.53'E, loc. 70-03, on boulders in deeper water, coll. K. & T. von Rintelen, 9 Oct. 2003; 6 ex. (ZMB 29054a, n=3; some SEM material; ZMB 29054b, n=3), west shore, at entrance to outlet bay, Cape Larona, 02°48.43'S, 121°24.75'E, loc. 73-03, (a) on boulders in deeper water, (b) on leaf litter, coll. K. & T. von Rintelen, 8 Oct. 2003; 6 ex. (MZB Cru. 1553, n=3; ZMB 29055, n=3, some SEM material), Loeha Island, north shore, 02°45.64'S, 121°34.32'E, loc. 97-03, on boulders in deeper water, coll. K. & T. von Rintelen, 4 Oct. 2003; 1 ex. (ZMB 29305), west shore, Cape Larona, 02°48.526'S, 121°25.044'E, loc. 120-04, on boulders in

deeper water, coll. K. & T. von Rintelen, 29 Jul.2004; 5 ex. (ZMB 29435, some SEM material), Loeha Island, north shore, 02°45.324'S, 121°32.019'E, loc. 226-05, on boulders in deeper water, coll. K. & T. von Rintelen, 23 Oct.2005; 9 ex. (MZB Cru. 1550), Loeha Island, southwest shore, 02°45.58'S, 121°31.14'E, loc. 149-04, on boulders in deeper water, coll. K. & T. von Rintelen, 5 Aug.2004; 2 ex. (MZB Cru. 1551), northeast shore, at Cape Noote, 02°39.751'S, 121°39.195'E, loc. 117-04, on boulders in deeper water, coll. K. & T. von Rintelen, 28 Jul.2004.

**Description.** – Carapace length 2.7-4.9 mm (n=35). Rostrum (Fig. 31A-C; Table 12) very long and slender, proximal part triangular widened, equally pronounced in male and female, reaching far beyond scaphocerite; 1.4-2.8 times as long as carapace (n=34), armed dorsally with 16-25 teeth, including 2-3 posterior to orbital margin, dorsal teeth throughout less densely spaced than ventral teeth, armed ventrally with 13-24 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.6-0.7 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.8-1.1 times as long as carapace (n=5), second segment 1.8-2.0 times length of third segment, third segment 0.2-0.3 times length of basal segment. Stylocerite reaching 0.9-1.0 times

length of antennular peduncle (n=5). Scaphocerite (Fig. 31E) 3.4-5.1 times as long as wide (n=22).

Sixth abdominal somite 0.7-1.0 times length of carapace (n=35), 1.5-2.1 times as long as fifth somite (n=22), 0.9-1.1 times length of telson (n=30). Telson (Fig. 31F,K) 3.4-4.0 times as long as wide (n=5), distal margin rounded, without projection, with 2-4 pairs of spinules and 1 pair of dorsolateral spinules (n=22); distal end with 4 pairs of spines, lateral pair distinctly longer than intermediate pairs, median pair shortest. Preanal carina (Fig. 31G) with a spine. Uropodal diaeresis (Fig. 31D) with 9-11 movable spinules (n=9).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipod absent from all pereopods. Incisor process of mandible (Fig. 32A) ending in a row of 2-3 small teeth, molar process truncated. Lower lacinia of maxillula (Fig. 32B) broadly rounded, upper lacinia elongate, with numerous distinct teeth and setae on inner margin, palp slender. Upper endites of maxilla (Fig. 32C) subdivided,

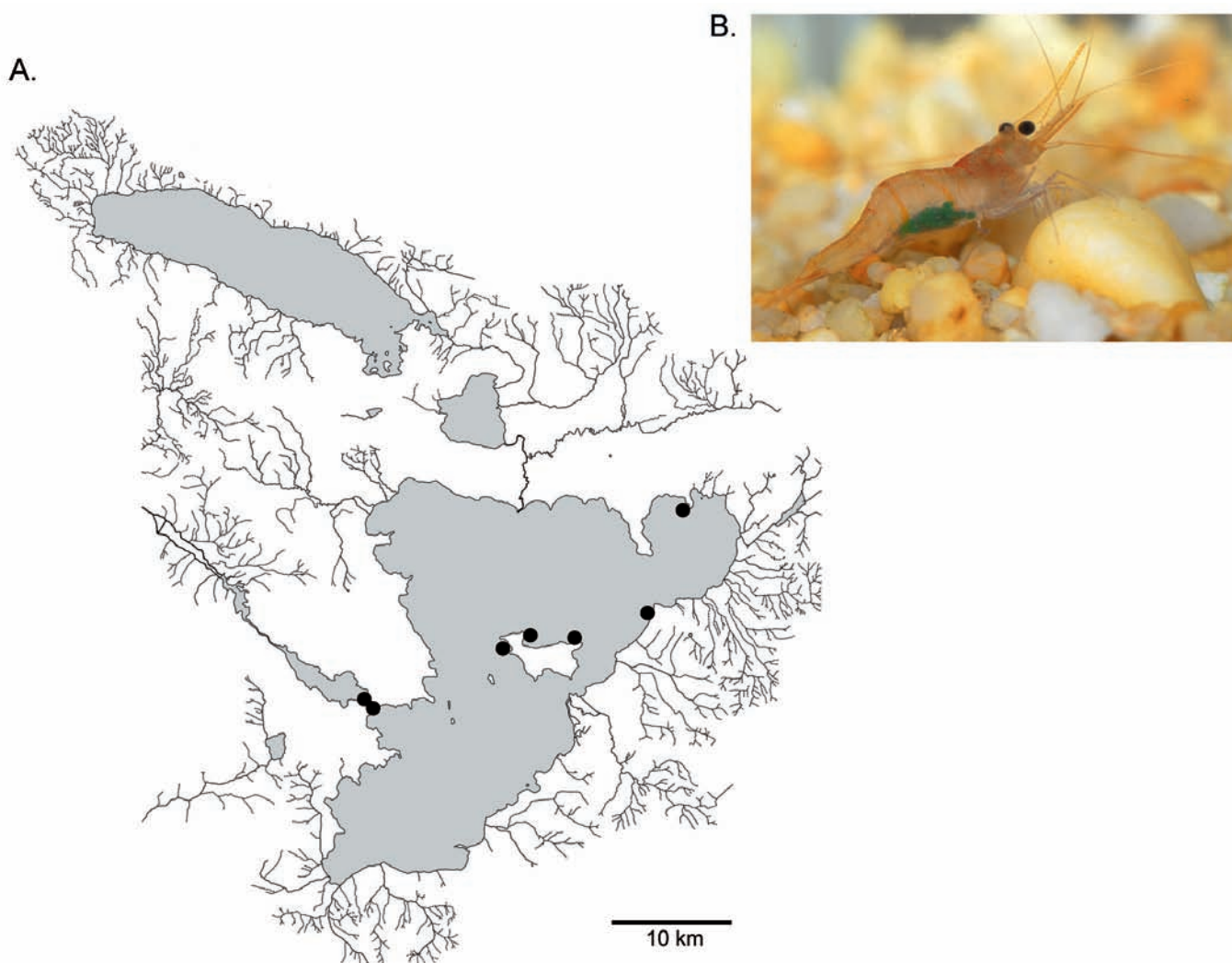


Fig. 30. *Caridina profundicola* from the Malili lake system. A. Distribution. B. Colour pattern of living animal (not to scale). Picture courtesy of Rainer Masche.

Table 12. Summary of standard morphometric parameters for *Caridina profundicola*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	2.7-4.9	3.9 $\pm$ 0.7	4.0	35
rl / cl	1.4-2.8	1.9 $\pm$ 0.3	1.9	34
n dorsal rostral teeth	16-25	20 $\pm$ 2	19	34
n ventral rostral teeth	13-24	20 $\pm$ 3	20	34
abds6 / cl	0.7-1.0	0.8 $\pm$ 0.1	0.8	35
abds6 / abds5	1.5-2.1	1.8 $\pm$ 0.1	1.8	22
abds6 / h tel	0.9-1.1	1.1 $\pm$ 0.1	1.1	30
h tel / w tel	3.4-4.0	3.7 $\pm$ 0.2	3.8	5
n spines uropodal diaeresis	9-11	10 $\pm$ 1	10	9
h ch1 / w ch1	2.9-4.4	3.5 $\pm$ 0.4	3.5	20
h ch1 / h ca1	0.8-1.1	0.9 $\pm$ 0.0	0.9	34
h ca1 / w ca1	4.2-5.6	5.1 $\pm$ 0.4	5.3	20
h ch2 / w ch2	4.3-6.1	5.1 $\pm$ 0.5	5.1	20
h ch2 / h ca2	0.6-0.7	0.6 $\pm$ 0.0	0.6	34
h ca2 / w ca2	8.8-12.2	10.8 $\pm$ 0.9	10.8	20
n spines p3	1-2	1 $\pm$ 0	1	16
n spines p5	34-44	39 $\pm$ 4	39	7

palp very slender, scaphognathite tapering posteriorly with numerous long, curved setae at posterior end. Distal end of palp of first maxilliped (Fig. 32D) triangular, with a long finger-like projection; flagellum of the exopod very elongated, endopod high, reaching half the flagellum of exopod in length. Second maxilliped (Fig. 32F) typical. Third maxilliped (Fig. 32E) with ultimate segment distinctly shorter than penultimate segment.

First and second pereopod very slender, chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig. 31M-O); chela of first pereopod 2.9-4.4 times as long as wide (n=20), 0.8-1.1 times length of carpus (n=34); tips of fingers rounded, without hooks; dactylus 1.0-1.3 times as long as palm (n=6); carpus 4.2-5.6 times as long as wide (n=20), 1.3-1.5 times length of merus (n=5). Chela of second pereopod 4.3-6.1 times as long as wide (n=20), 0.6-0.7 times length of carpus (n=34); tips of fingers rounded, without hooks, dactylus 1.1-1.2 times as long as palm (n=6); carpus 8.8-12.2 times as long as wide (n=20), 1.3-1.6 times as long as merus (n=5).

Third pereopod (Fig. 31I,L) slender, dactylus 5.8-7.8 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 1-2 accessory spines on flexor margin (n=16); propodus 14.0-19.0 times as long as wide (n=5), 3.2-4.1 times as long as dactylus; carpus 6.9-8.2 times as long as wide, 0.6 times as long as propodus, 0.4-0.5 times as long as merus; merus 11.5-15.7 times as long as wide, bearing 3-4 strong, movable spines on posterior margin of outer surface.

Fifth pereopod slender (Fig. 31H,J), dactylus 6.2-8.3 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 34-44 (n=7) accessory spines on flexor margin; propodus

20.4-22.8 times as long as wide (n=5), 3.6-4.6 times as long as dactylus; carpus 6.6-9.3 times as long as wide, 0.5 times as long as propodus, 0.5-0.6 times as long as merus; merus 10.7-14.3 times as long as wide, bearing 3 strong, movable spines on posterior margin of outer surface (n=2).

Endopod of male first pleopod (Fig. 31P) elongated triangular, 1.8-2.2 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 31Q) 0.8-1.0 times length of appendix masculina (n=5).

Ovigerous females with 41-80 eggs (n=9 females); egg size 0.7-0.9 x 0.4-0.6 mm (n=202, eggs with and without eyes).

**Distribution.** – Endemic to Lake Towuti (Fig. 30A).

**Biology and ecology.** – *C. profundicola* is a hard substrate dweller. Adult specimens of this species were exclusively found in deeper water regions, approx. below 3 m, although two juveniles were collected among leaf litter in shallow water. The majority of species was found between large rocks (boulders), often together with *C. spinata*. *C. profundicola* is a rather inactive species, which keeps still when disturbed (KvR pers. observation), although it is capable of very fast movements if necessary.

**Colour pattern.** – Body and appendages yellowish-transparent, sometimes slightly red, usually with two conspicuous yellow transversal stripes on the abdomen (Fig. 30B). Eggs green, contrasting the body colour. The yellow stripes are also already distinctive in juveniles.

**Etymology.** – *Caridina profundicola* refers to the unusually deep occurrence of this new species in the Malili lake system.



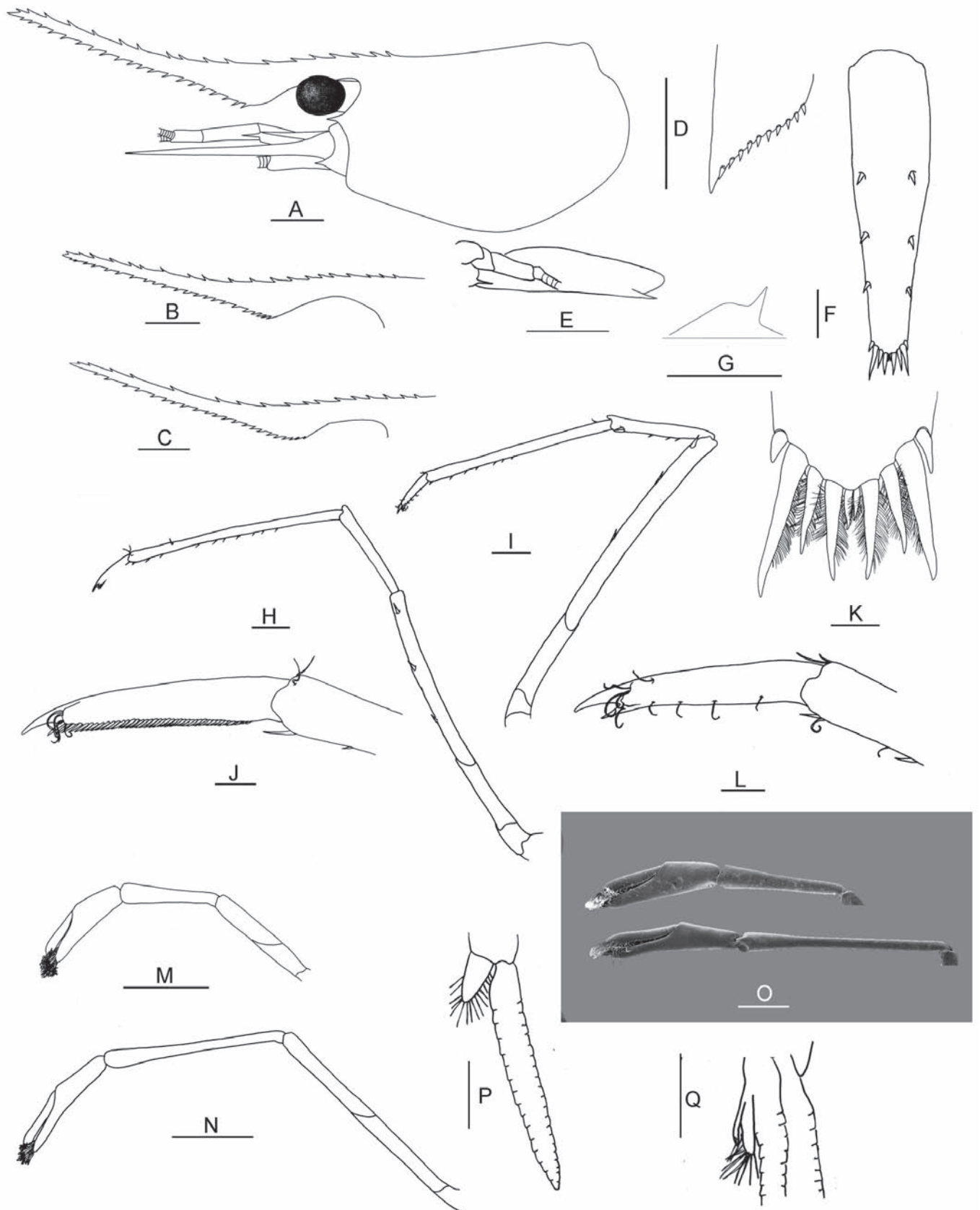


Fig. 31. *Caridina profundicola* from the Malili lake system. A. Cephalothorax and cephalic appendages, female (ZMB 29025); B. Rostrum, other female (ZMB 29025); C. Rostrum, female (ZMB 29054a); D. Uropodal diaeresis, female (ZMB 29025); E. Scaphocerite, male (ZMB 29025); F. Telson, female (ZMB 29025); G. Preanal carina; H. Fifth pereiopod; I. Third pereiopod; J. Dactylus of fifth pereiopod; K. Distal end of telson; L. Dactylus of third pereiopod; M. First pereiopod, female (ZMB 29054a); N. Second pereiopod; O. SEM image of chela and carpus of first and second pereiopods, female (ZMB 29025); P. Endopod of male first pleopod (ZMB 29025); Q. Appendix masculina of male second pleopod. Scale bars: A-C, E = 1.0 mm; D, J-L = 0.1 mm; F-I, M-Q = 0.5 mm.

The name is a combination of the Latin words *profundus* (depths) and *collere* (to inhabit).

**Taxonomic remarks.** – *C. profundicola* differs from all Malili species by the characteristic triangular shape of the proximal part of the otherwise very slender rostrum. A similar triangular shape is only pronounced in *C. lingkonae*, but differs by a distinctly more slender and also longer rostrum compared to carapace length (1.4-2.8, median 1.9 vs. 1.0-1.6, median 1.2 in *C. lingkonae*), and a higher number of ventral teeth (13-24, median 20 vs. 7-18, median 12 in *C. lingkonae*).

*C. profundicola* (2.7-4.9 mm, median 4.0 mm) and *C. spinata* (carapace length 3.0-5.0 mm, median 4.2 mm) are the largest lacustrine species in the Malili system. Both show similar

slender pereopods and often occur on the same substrate (usually boulders in deeper water) at the same locality, but differ in the shape of the rostrum (proximal part triangular while distal part distinctly slender vs. not triangular, but rather uniformly slender in *C. spinata*), a longer rostrum compared to the carapace length (1.4-2.8, median 1.9 vs. 0.9-1.7, median 1.2 in *C. spinata*), a larger number of ventral teeth on the rostrum (13-24, median 20 vs. 5-12, median 9 in *C. spinata*) and on the dactylus of the fifth pereopod (34-44, median 39 vs. 25-31, median 29 in *C. spinata*), respectively, and a lower number of spines on the uropodal diaeresis (9-11, median 10 vs. 12-16, median 14 in *C. spinata*). Both species differ in their behaviour: *C. profundicola* is distinctly more inactive and can almost be caught by hand, while *C. spinata* always appears rather active. With its extremely long

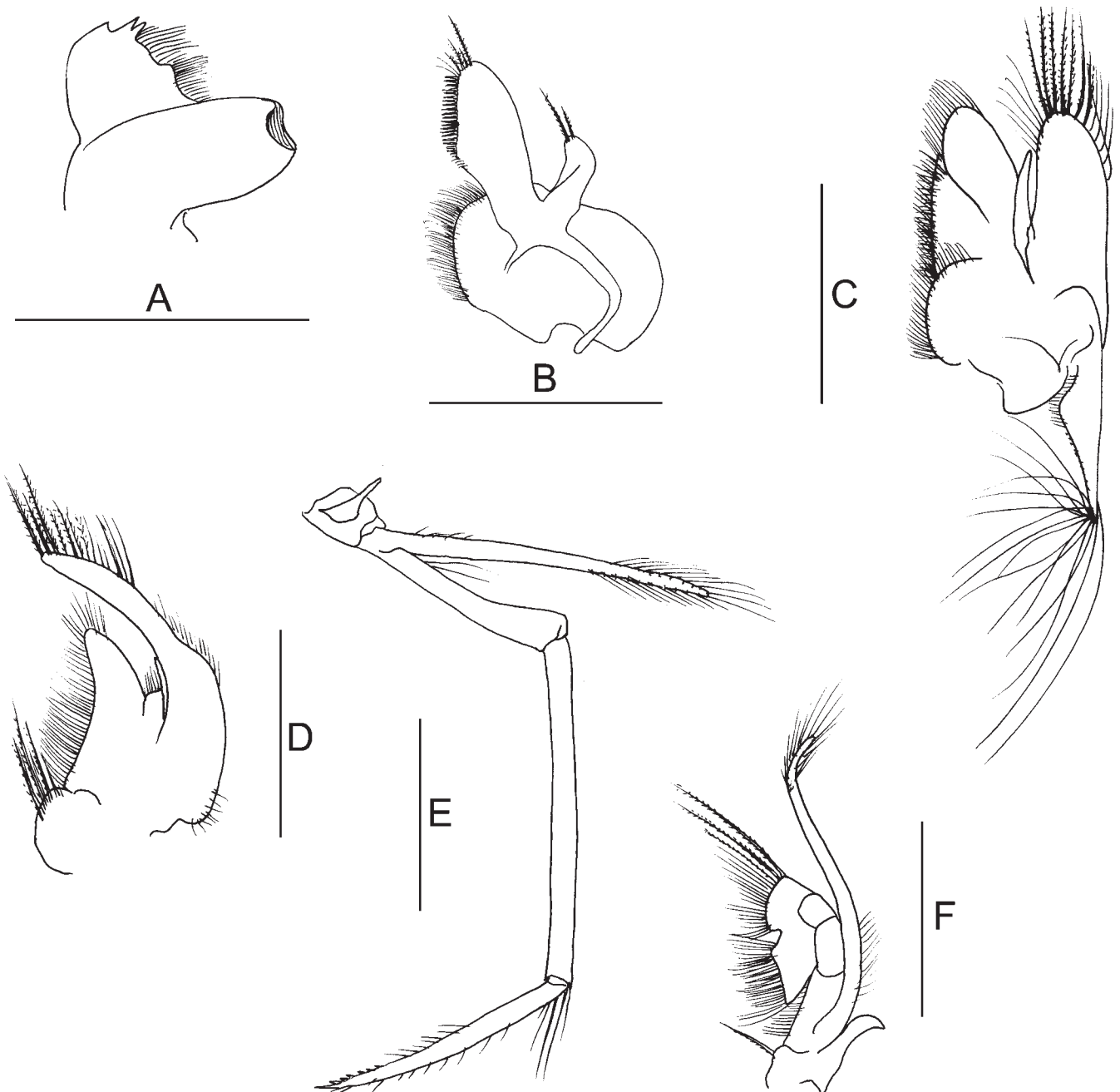


Fig. 32. *Caridina profundicola* from the Malili lake system. A. Mandible (MZB Cru 1552); B. Maxillula; C. Maxilla; D. first maxilliped; E. third maxilliped; F. second maxilliped. Scale bars: A-F = 1mm.

and slender rostrum, *C. profundicola* further resembles *C. ensifera* and *C. caerulea* from Lake Poso, but differs in the triangular shape and the constant denticulation (vs. always with an unarmed gap in both Poso species).

In the molecular phylogeny (Figs. 63–64), *C. profundicola* is genetically distinct from all other ancient lake species.

***Caridina spinata* Woltereck, 1937a**

(Figs. 33–35; Table 13)

*Caridina spinata* Woltereck, 1937a: 221, fig. I.3, pls. 3,6 (type locality: Lake Towuti, Lake Matanno [Matano]).

*Caridina spinata* – Woltereck, 1937b: 302, fig. 8; Chace, 1997: 20; von Rintelen et al., 2008: 2244, Table 1; Cai et al., 2009: 25, Fig. 6 (type locality of neotype: Lake Towuti, about 3 km south of Timampu, estuary of Sungei [River] Batuopa).

*Cardina spinata* – Brooks, 1950: 168 (erroneous spelling).

**Not:** *Caridina spinata* – von Rintelen et al., 2007b: 262, fig. 2b.

**Material examined.** – Lake Towuti: 19 ex. (MZB Cru 1555, n=10 and ZMB 29026, n=9, some SEM material), west shore, at entrance to outlet bay, Cape Laron, 02°48.43'S, 121°24.75'E, loc. 73-03, coll. K. & T. von Rintelen, 8 Oct.2003; 1 ex. (ZMB 29056, n=1 and few juveniles, some SEM material), east shore, south of Cape Tomeraka, 02°44.47'S, 121°37.53'E, loc. 70-03, coll. K. & T. von Rintelen, 27 Sep.2003; 1 ex. (ZMB 29057, n=1 and few juveniles), southwest shore, west of Cape Tetetu, 02°54.13'S, 121°23.78'E, loc. 76-03, coll. K. & T. von Rintelen, 28 Sep.2003; 1 ex. (ZMB 29058, some SEM material), Loeha Island, north shore, 02°45.64'S, 121°34.32'E, loc. 97-03, coll. K. & T. von Rintelen, 4 Oct.2003; (ZMB 29141, n=few juveniles), south shore, approx. 2 km east of Cape Mea, 02°55.8'S, 121°26.92'E, loc. 74-03, coll. K. & T. von Rintelen, 28 Sep.2003; (ZMB 29142, n=few juveniles), north shore, bay east of Cape Bintu, 02°39.48'S, 121°33.25'E, loc. 68-03, coll. K. & T. von Rintelen, 26 Sep.2003; 1 ex. (ZMB 29154), Laron River, close to outlet bay, 02°45.8'S, 121°20.8'E, loc. 51-03, coll. K. & T. von Rintelen, 28 Jul.2004; 2 ex. (ZMB 29434), Loeha Island, north shore, 02°45.324'S, 121°32.019'E, loc. 226-05, coll. K. & T. von Rintelen, 23 Oct.2005; 6 ex. (MZB Cru 1556), northeast shore, at Cape Noote, 02°39.751'S, 121°39.195'E, loc. 117-04, coll.

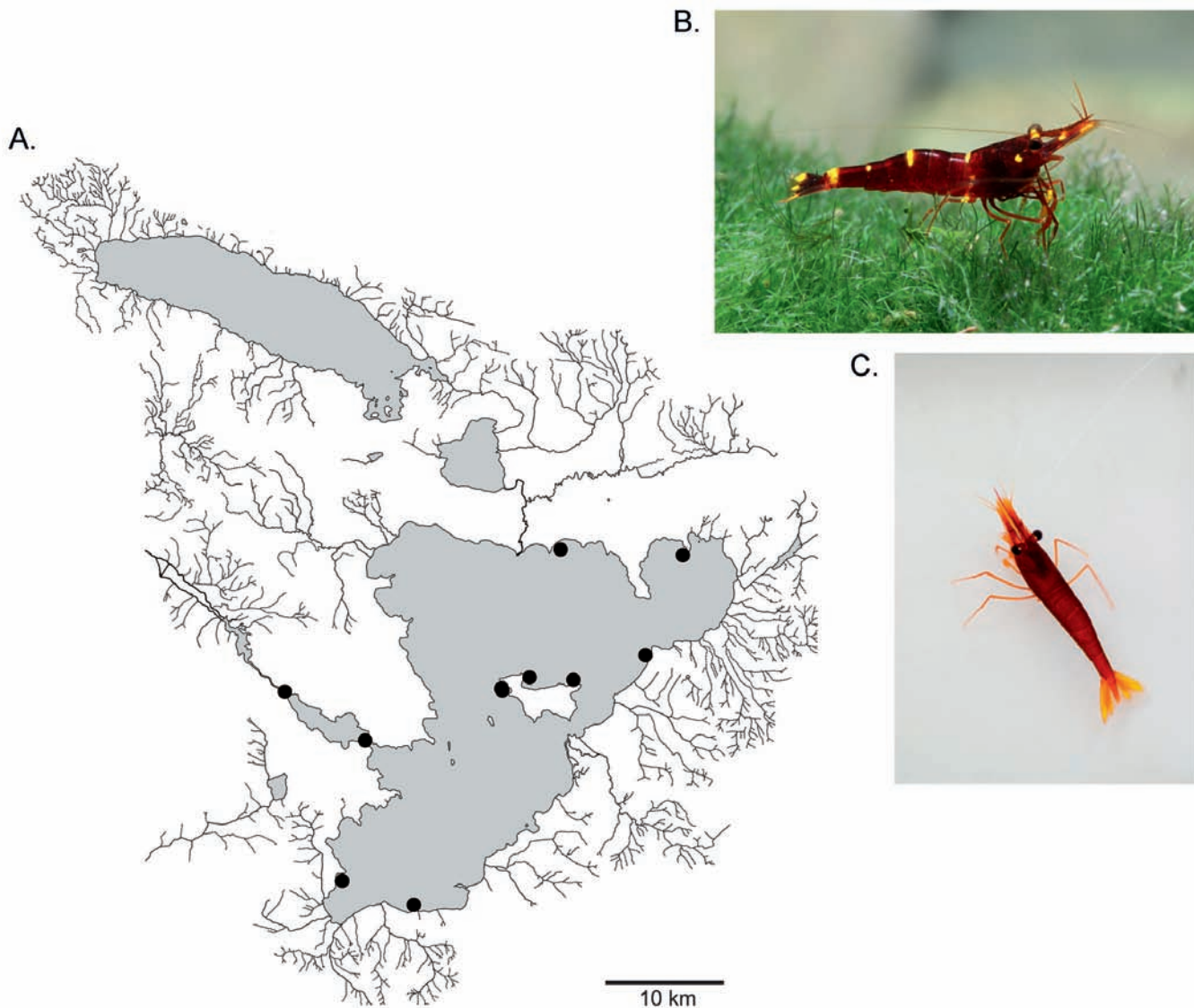


Fig. 33. *Caridina spinata* from the Malili lake system. A. distribution. B,C. colour pattern of living animals (not to scale). Picture B. courtesy of Chris Lukhaup.

Table 13. Summary of standard morphometric parameters for *Caridina spinata*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	3.0-5.0	4.1 $\pm$ 0.6	4.2	17
rl / cl	0.9-1.7	1.3 $\pm$ 0.2	1.2	16
n dorsal rostra teeth	14-24	17 $\pm$ 3	17	16
n ventral rostral teeth	5-12	8 $\pm$ 2	9	16
abds6 / cl	0.5-0.7	0.6 $\pm$ 0.0	0.6	18
abds6 / abds5	1.5-1.9	1.7 $\pm$ 0.1	1.7	11
abds6 / h tel	0.8-1.0	0.9 $\pm$ 0.0	0.9	12
h tel / w tel	3.2-3.6	3.3 $\pm$ 0.1	3.3	6
n spines uropodal diaeresis	12-16	14 $\pm$ 1	14	6
h ch1 / w ch1	2.0-3.6	2.8 $\pm$ 0.6	3.0	13
h ch1 / h ca1	0.9-1.4	1.1 $\pm$ 0.2	1.0	18
h ca1 / w ca1	2.1-5.2	3.7 $\pm$ 1.3	4.5	12
h ch2 / w ch2	2.3-5.5	3.8 $\pm$ 1.1	4.3	13
h ch2 / h ca2	0.5-0.8	0.6 $\pm$ 0.1	0.6	17
h ca2 / w ca2	4.8-11.9	8.4 $\pm$ 2.6	9.6	13
n spines p3	2-3	2 $\pm$ 0	2	5
n spines p5	25-31	29 $\pm$ 2	29	5

K. & T. von Rintelen, 28 Jul.2004; 1 ex. (MZB Cru 1557), Loeha Island, southwest shore, 02°45.58'S, 121°31.14'E, loc. 149-04, coll. K. & T. von Rintelen, 5 Aug.2004; 2 ex. (MZB Cru 1558, n=2 juveniles), Loeha Island, west shore, 02°45.5'S, 121°31.06'E, loc. 95-03, coll. K. & T. von Rintelen, 5 Aug.2004.

**Description.** – Carapace length 3.0-5.0 mm (n=17). Rostrum (Fig. 34A-B, Table 13) long, reaching beyond or far beyond end of scaphocerite, 0.9-1.7 times as long as carapace (n=16), armed dorsally with 14-24 teeth (including 3-5 teeth posterior to orbital margin), anterior less densely spaced, armed ventrally with 5-12 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.6 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.9-1.0 times as long as carapace (n=5), second segment 1.4-2.0 times length of third segment, third segment 0.3-0.4 times length of basal segment. Stylocerite reaching 0.9-1.0 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 34F) 3.3-5.4 times as long as wide (n=5).

Sixth abdominal somite 0.5-0.7 times length of carapace (n=18), 1.5-1.9 times as long as fifth somite (n=11), 0.8-1.0 times length of telson (n=12). Telson (Fig. 34E,I) 3.2-3.6 times as long as wide (n=6), distal margin rounded, without projection, with 3-4 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 3 pairs of spines, lateral pair distinctly longer than intermediate pairs, median pair or median spine shortest. Preanal carina (Fig. 34C) with a spine. Uropodal diaeresis (Fig. 34D) with 12-16 movable spinules (n=6).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair

of podobranchs on second maxilliped reduced strongly to a laminate form. Epipod present on first pereopod. Incisor process of mandible (Fig. 35A) ending in a row of 3-4 small teeth, molar process truncated. Lower lacinia of maxillula (Fig. 35B) broadly rounded, upper lacinia elongated, with numerous distinct teeth and setae on inner margin, palp slender. Upper endites of maxilla (Fig. 35C) subdivided, palp short, scaphognathite tapering posteriorly with numerous long, curved setae at posterior end. Distal end of palp of first maxilliped (Fig. 35F) triangular, with a finger-like projection; flagellum of the exopod very elongated, endopod high, reaching half the flagellum of exopod in length. Second maxilliped (Fig. 35E) typical. Third maxilliped (Fig. 35D) with ultimate segment distinctly shorter than penultimate segment.

Chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig. 34N-P); chela of first pereopod 2.0-3.6 times as long as wide (n=13), 0.9-1.4 times length of carpus (n=18); tips of fingers rounded, without hooks; dactylus 1.3-1.5 times as long as palm (n=5); carpus 2.1-5.2 times as long as wide (n=12), 1.2-1.5 times length of merus (n=5). Chela of second pereopod 2.3-5.5 times as long as wide (n=13), 0.5-0.8 times length of carpus (n=17); tips of fingers rounded, without hooks, dactylus 1.3-1.6 times as long as palm (n=5); carpus 4.8-11.9 times as long as wide (n=13), 1.4-1.6 times as long as merus (n=5).

Third pereopod (Fig. 34G,K) slender, dactylus 2.8-4.0 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 2-3 accessory spines on flexor margin; propodus 17.0-23.0 times as long as wide, 7.0-7.8 times as long as dactylus; carpus 6.8-8.9 times as long as wide, 0.5-0.6 times as long as propodus, 0.5-0.6 times as long as merus; merus 10.0-13.4

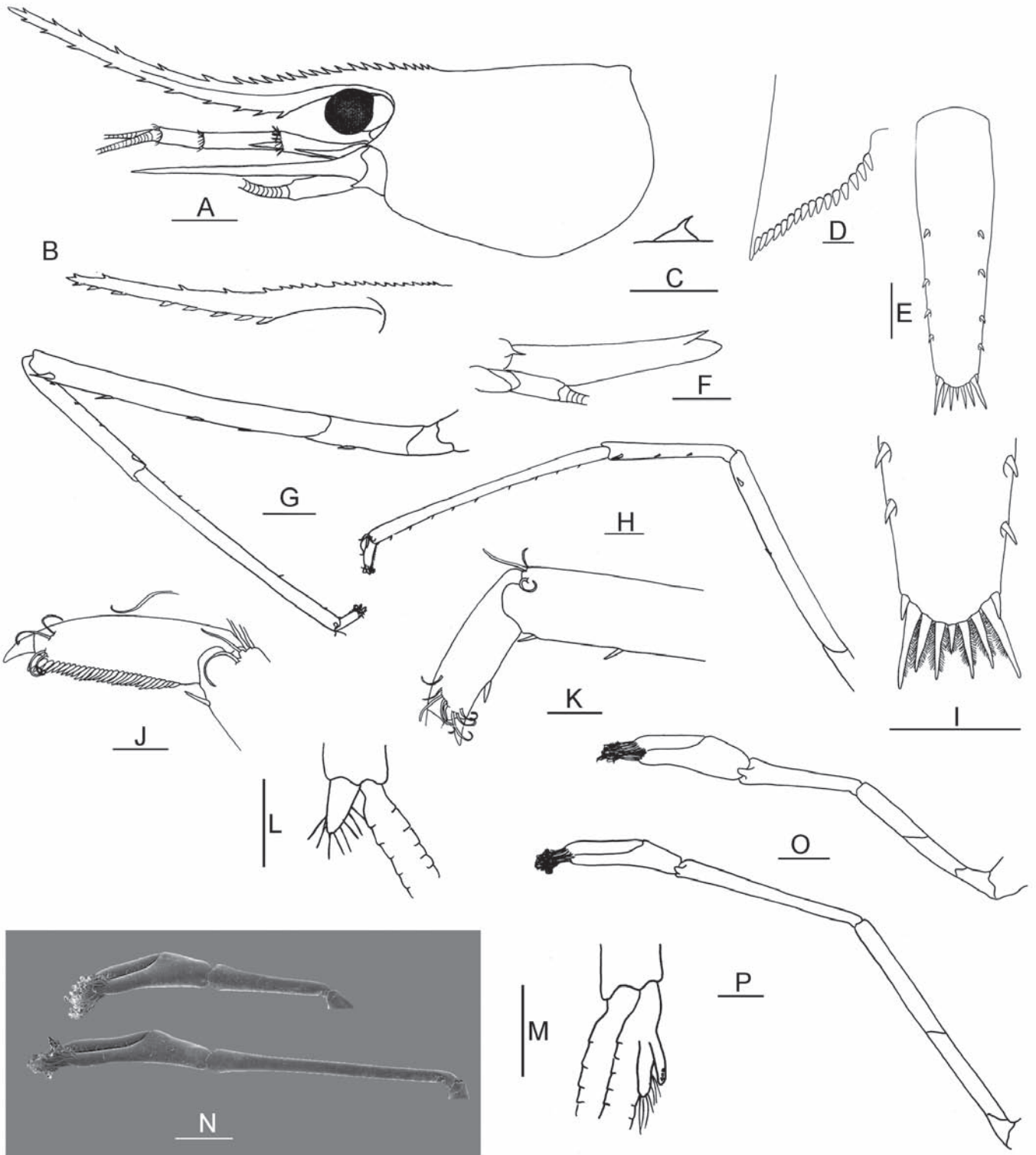


Fig. 34. *Caridina spinata* from the Malili lake system. A. Cephalothorax and cephalic appendages, male (ZMB 29026); B. Woltereck's drawing of the rostrum (modified from 1937a); C. Preanal carina, male (MZB Cru. 1556); D. Uropodal diaeresis, male (ZMB 29026); E. telson; F. Scaphocerite, male (MZB Cru. 1556); G. Third pereiopod, female (ZMB 29026); H. Fifth pereiopod; I. Distal end of telson, male (ZMB 29026); J. Dactylus of fifth pereiopod, female (ZMB 29026); K. Dactylus of third pereiopod; L. Endopod of male first pleopod (MZB Cru. 1556); M. Appendix masculina of male second pleopod; N. SEM image of chela and carpus of first and second pereiopods, female (ZMB 29058); O. First pereiopod, male (ZMB 29026); P. Second pereiopod. Scale bars: A, F = 1.0 mm; C, E, G-I, L-P = 0.5 mm; D, J-K = 0.1 mm; B = no scale available.

times as long as wide, bearing 3-4 strong, movable spines on posterior margin of outer surface.

Fifth pereopod slender (Fig. 34H,J), dactylus 3.6-5.4 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 25-31 accessory spines on flexor margin; propodus 18.7-26.3 times as long as wide, 3.9-7.6 times as long as dactylus; carpus 6.9-8.7 times as long as wide, 0.5-0.6 times as long

as propodus, 0.6-0.7 times as long as merus; merus 9.2-11.8 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 34L) elongated triangularly, 1.8-1.9 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 34.M) 0.7-0.9 times length of appendix masculina (n=5).

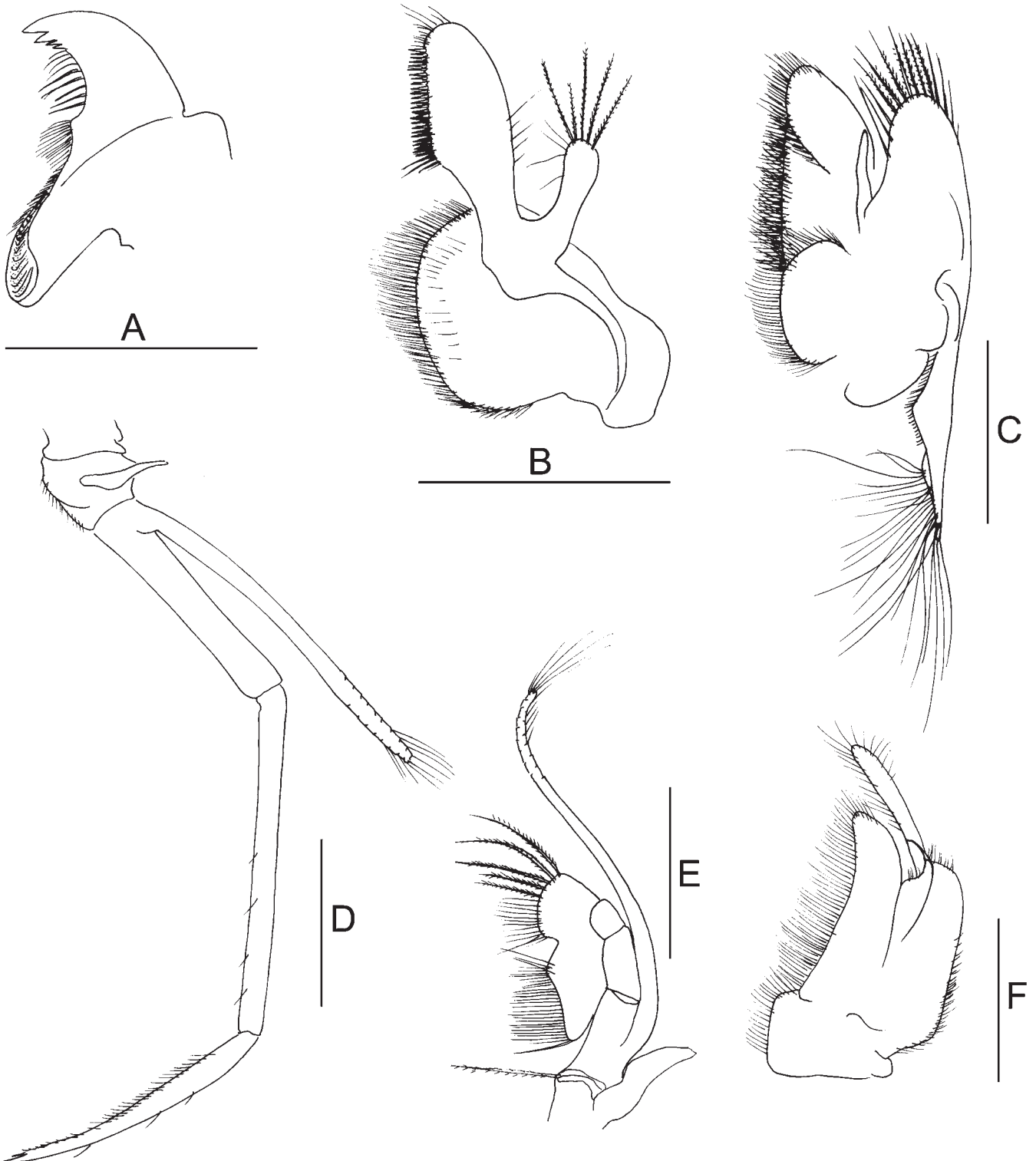


Fig. 35. *Caridina spinata* from the Malili lake system. A. Mandible (MZB Cru 1555); B. Maxillula; C. Maxilla; D. third maxilliped; E. second maxilliped; F. first maxilliped. Scale bars: A-F = 1mm.

Ovigerous females with 17-31 eggs (n=3 females); egg size 1.0-1.1 x 0.6-0.7 mm (n=37, eggs with and without eyes).

**Distribution.** – Endemic to Lake Towuti and widely distributed within the lake (Fig. 33A).

**Biology and ecology.** – *C. spinata* is a hard substrate dweller on rocks. Whereas juveniles were also frequently observed in shallow water zones (above approx. 3-5 m), adults seem to prefer boulders in deeper water zones, where they often occur in syntopy with *C. profundicola* and sometimes with other rock dwellers from Lake Towuti. When disturbed, *C. spinata* tries to hide in nearby gaps between rocks (usually boulders). Like in other typical rock dwellers from the Malili lakes it rather escapes side- or downwards than in other directions.

**Colour pattern.** – Body and appendages mainly crimson to deep red (Fig. 33B-C), often with two to three bright yellow or orange transversal stripes at the end of the carapace and the abdomen and a few dots of the same colour on various body parts or body appendages, e.g. tips of the uropods. Chelae and uropods can be completely yellow or orange. This combination of red-crimson and yellow or orange is unique in the ancient lake species, although a red body colouration is common in rock dwellers. Antennules usually transparently white. Eggs coloured as body. This colour pattern remains visible even if the shrimp is under stress, the intensity of the colour might fade.

**Taxonomic remarks.** – Cai et al. (2009: 19) stated: “Specimens of Woltereck (1937a, b) are no longer extant [...]. As all new species described by Woltereck are morphologically close to each other and to stabilize the taxonomic status of those species, neotypes are designated if specimens are available from the recent collections”. Consequently, they designated a neotype for *C. spinata* from Lake Towuti (ovigerous female, cl 4.3 mm, ZRC) (2009: 25).

In living animals the colour pattern of *C. spinata* always distinguishes it from all other species. *C. spinata* (carapace length 3.0-5.0 mm, median 4.2 mm) and *C. profundicola* (2.7-4.9 mm, median 4.0 mm) are the largest lacustrine species in the Malili lakes. Both have similarly slender pereopods and often occur on the same substrate (usually boulders in deeper water) at the same locality. They differ in the shape of the rostrum (not triangular, but rather uniformly slender vs. proximal part triangular while distal part distinctly slender in *C. profundicola*), a shorter rostrum compared to the carapace length (0.9-1.7, median 1.2 vs. 1.4-2.8, median 1.9 in *C. profundicola*), a smaller number of ventral teeth on the rostrum (5-12, median 9 vs. 13-24, median 20 in *C. profundicola*) and on the dactylus of the fifth pereopod (25-31, median 29 vs. 34-44, median 39 in *C. profundicola*), as well as a higher number of spines on the uropodal diaeresis (12-16, median 14 vs. 9-11, median 10 in *C. profundicola*). With regard to the rostrum, *C. spinata* resembles *C. striata*, *C. glaubrechti* and *C. woltereckae*, but it differs in the slender form of the first and second pereopods and the generally

larger size (carapace length up to 5.0 mm vs. not larger than 3.4-3.8 mm in the other species).

In the molecular phylogeny (Figs. 63-64), *C. spinata* is genetically distinct from all other ancient lake species.

### *Caridina spongicola* Zitzler & Cai, 2006

(Figs. 36-38; Table 14)

*Caridina spongicola* Zitzler & Cai, 2006: 271, Figs. 1-3. (type locality: outlet bay of Lake Towuti)

*Caridina spongicola* – von Rintelen et al., 2007b: 262, Figs. 1, 2008: 2244, Table 1.

**Material examined.** – Holotype: ovigerous female (eggs without eyes), cl 2.4 mm (MZB Cru 1559), Lake Towuti, west shore, outlet bay, west of Cape Tokaluku, 02°47.261'S, 121°23.17'E, loc. 119-04, on sponge, coll. K. & T. von Rintelen, 29 Jul.2004.

Paratypes (Lake Towuti) – 3 females (cl 2.0-2.4 mm) (MZB Cru 1560); 2 ovigerous females (cl 2.4-2.8 mm) (MZB Cru 1560), same data as holotype; 5 males (cl 1.8-2.3 mm)(MZB Cru 1560), same data as holotype; 11 females (cl 1.9-2.6 mm)(ZMB 29027, some SEM material), 2 ovigerous females (cl 2.4 mm)(ZMB 29027, some SEM material), Lake Towuti, west shore, outlet bay, west of Cape Tokaluku, 02°47.32'S 121°23.38'E, loc. 52-03, on sponge, coll. K. & T. von Rintelen, 21 Sep.2003; 4 males (cl 1.9-2.1 mm)(ZMB 29027, some SEM material), same data as previous sample; 9 males (cl 2.1-2.4 mm), 12 females (cl 2.2-2.6 mm), 6 ovigerous females (cl 2.4-2.6 mm)(ZRC 2006.0114), Lake Towuti, west shore, outlet bay, west of Cape Tokaluku, 02°46.277'S 121°21.83'E, loc. 02-05, on sponge, coll. Y. Cai, K. & T. von Rintelen, 3 Jan.2005.

Others (Lake Towuti) – 170 ex. (MZB Cru 1845, n=75 ;ZMB 29125, n=95 and several juveniles), same data as paratypes of ZRC 2006.0114, loc. 02-05, on sponge; 23 ex. (ZMB 29313, n=23 and several juveniles), west shore, outlet bay, 02°47.345'S, 121°23.356'E, loc. 14-05, on sponge, coll. K. & T. von Rintelen, 9 Jan.2005; 12 ex. (ZMB 29129, n=12 and several juveniles), west shore, outlet bay, 02°47.623'S, 121°22.724'E, loc. 13-05, on sponge, coll. K. & T. von Rintelen, 9 Jan.2005; (ZMB 29294, several juveniles), same data as holotype, loc. 119-04, on sponge.

**Description.** – Carapace length 1.8-2.8 mm (n=48). Rostrum (Figs. 36B, 37.A, 38.A; Table 14) short, straight and slender, anterior third slightly upturned, reaching to or slightly beyond third segment of antennular peduncle, 0.7-3.0 times as long as carapace (n=48), armed dorsally with 14-25 teeth (including 3-5 teeth posterior to orbital margin), anterior less densely spaced, armed ventrally with 3-15 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end reaching to or beyond half length of basal segment of antennular peduncle. Antennular peduncle 0.8-1.2 times as long as carapace (n=10), second segment 2.0-2.3 times length of third segment, third segment 0.2-0.3 times length of basal segment (n=5). Stylocerite reaching 0.8-0.9 length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 37C) slender, 3.5-5.0 times as long as wide (n=8).

Sixth abdominal somite 0.5-0.7 times length of carapace (n=48), 1.2-2.3 times as long as fifth somite (n=21), 0.7-

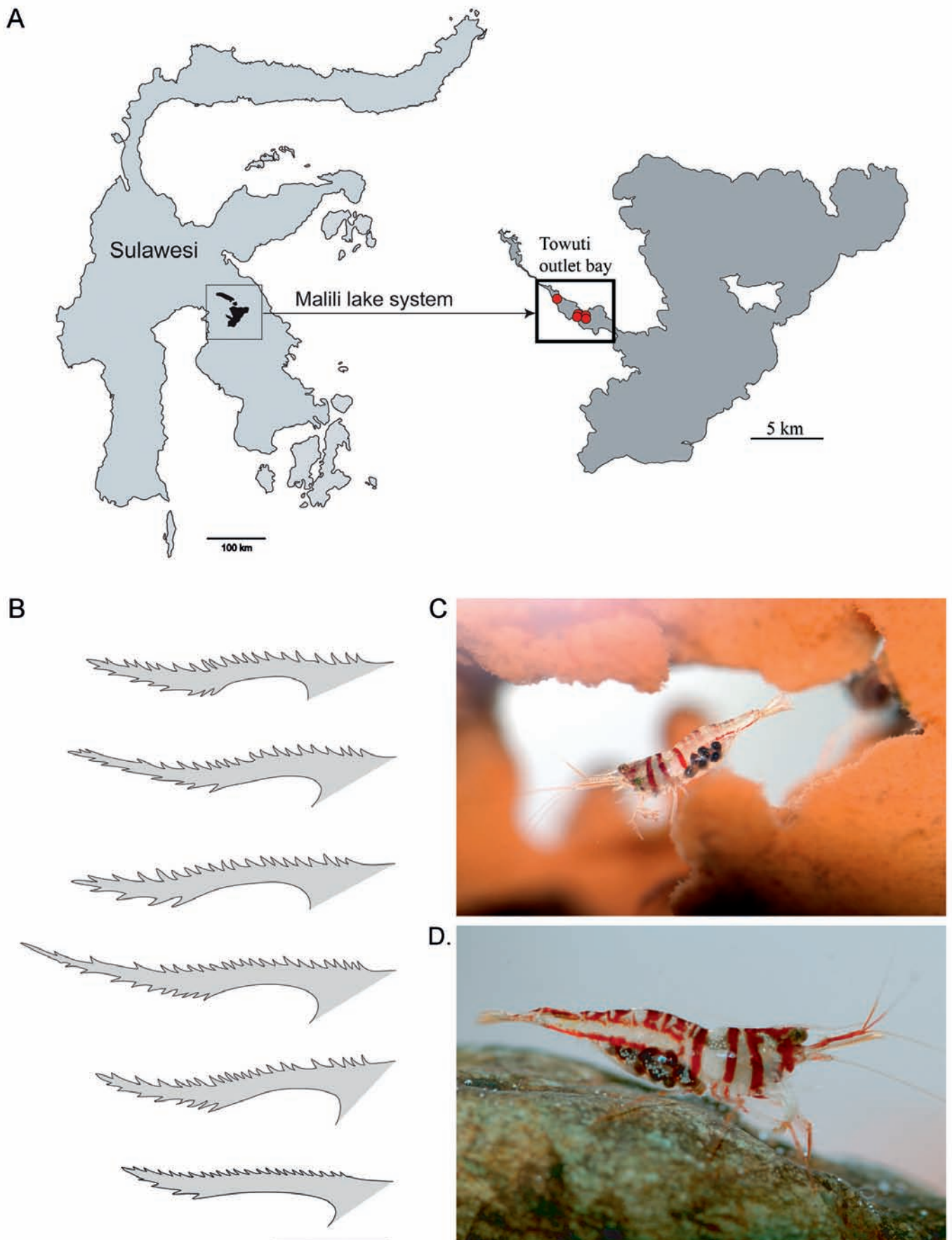


Fig. 36. *Caridina spongicola* from the Malili lake system. A. Distribution. B. Rostrum variability (ZMB 29027). C.-D. Colour pattern of living animals (not to scale). Figure from Zitzler & Cai (2006), i.e. by the same authors.



Table 14. Summary of standard morphometric parameters for *Caridina spongicola*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	1.8-2.8	2.3 $\pm$ 0.3	2.4	48
rl / cl	0.7-3.0	1.6 $\pm$ 0.8	1.2	48
n dorsal rostral teeth	14-25	20 $\pm$ 2	20	48
n ventral rostral teeth	3-15	6 $\pm$ 2	6	48
abds6 / cl	0.5-0.7	0.6 $\pm$ 0.1	0.6	48
abds6 / abds5	1.2-2.3	1.9 $\pm$ 0.3	1.9	21
abds6 / h tel	0.7-1.0	0.9 $\pm$ 0.1	0.9	28
h tel / w tel	2.8-4.1	3.4 $\pm$ 0.3	3.4	13
n spines uropodal diaeresis	10-12	11 $\pm$ 1	11	12
h ch1 / w ch1	2.3-2.9	2.6 $\pm$ 0.2	2.7	20
h ch1 / h ca1	0.8-1.4	1.2 $\pm$ 0.1	1.2	48
h ca1 / w ca1	2.5-3.5	2.9 $\pm$ 0.3	3.0	20
h ch2 / w ch2	3.0-4.0	3.4 $\pm$ 0.3	3.3	20
h ch2 / h ca2	0.7-0.8	0.8 $\pm$ 0.0	0.8	46
h ca2 / w ca2	5.9-7.9	6.6 $\pm$ 0.5	6.6	20
n spines p3	1-3	2 $\pm$ 1	2	7
n spines p5	21-31	26 $\pm$ 4	27	7

1.0 times length of telson (n=28). Telson (Fig. 37D,F) 2.8-4.1 times as long as wide (n=13), distal margin rounded, without projection, with 3-4 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 4 pairs of spines, lateral pair distinctly longer than intermediate pairs, median pair shortest. Preanal carina (Fig. 37B) rounded, without spine. Uropodal diaeresis (Fig. 37E) with 10-12 movable spinules (n=12).

Incisor process of mandible (Fig. 38B) ending in irregular teeth, molar process truncated. Lower lacinia of maxillule (Fig. 38C) broadly rounded, upper lacinia elongated, with a number of distinct teeth on inner margin, palp slender. Upper endites of maxilla (Fig. 38G) subdivided, palp elongate, scaphognathite tapering posteriorly. Palp of first maxilliped (Fig. 38D) truncate, ending in triangular shape. Podobranch of second maxilliped (Fig. 38F) reduced to small lamina. Third maxilliped (Fig. 38E) with ultimate segment slightly shorter than penultimate segment.

Chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig. 37K-M); chela of first pereopod 2.3-2.9 times as long as wide (n=20), 0.8-1.4 times length of carpus (n=48); tips of fingers rounded, without hooks; dactylus 1.2-1.5 times as long as palm (n=5); carpus 2.5-3.5 times as long as wide (n=20), 1.2-1.5 times length of merus (n=5). Chela of second pereopod 3.0-4.0 times as long as wide (n=20), 0.7-0.8 times length of carpus (n=46); tips of fingers rounded, without hooks, dactylus 1.3-1.7 times as long as palm (n=5); carpus 5.9-7.9 times as long as wide (n=20), 1.4-1.6 times as long as merus (n=5).

Third pereopod (Fig. 37G-H) slender, dactylus 3.0-5.8 times as long as wide (terminal spine included, without spines of

flexor margin; n=5), terminating in one large claw with 1-3 accessory spines on flexor margin (n=7); propodus 11.1-15.0 times as long as wide, 3.3-5.3 times as long as dactylus; carpus 5.0-6.1 times as long as wide, 0.5-0.7 times as long as propodus, 0.5 times as long as merus; merus 8.1-10.0 times as long as wide, bearing 2-4 strong, movable spines on posterior margin of outer surface.

Fifth pereopod slender (Fig. 37I-J), dactylus 3.5-4.4 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 21-31 accessory spines on flexor margin (n=7); propodus 13.1-15.0 times as long as wide, 3.6-4.5 times as long as dactylus; carpus 4.6-5.9 times as long as wide, 0.4-0.5 times as long as propodus, 0.6 times as long as merus; merus 7.1-9.0 times as long as wide, bearing 2 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 38H) elongated triangular, 2.0-2.8 times as long as proximally wide (n=5), without appendix interna, appendix interna of male second pleopod (Fig. 38I) not reaching end of appendix masculina.

Ovigerous females with 12-18 eggs (n=4 females); egg size 0.8-0.9 x 0.4-0.6 mm (n=53, eggs with and without eyes).

**Distribution.** – *Caridina spongicola* is endemic to Lake Towuti and so far only known from the outlet bay, where its sponge host occurs (Fig. 36A; Zitzler & Cai, 2006).

**Biology and ecology.** – During an extensive substrate specific sampling in the Malili lake system in 2003, 2004, and 2005, *Caridina spongicola* was exclusively found on a currently undescribed freshwater sponge of the suborder Spongillina. It grows in the outlet of lake Towuti at depths

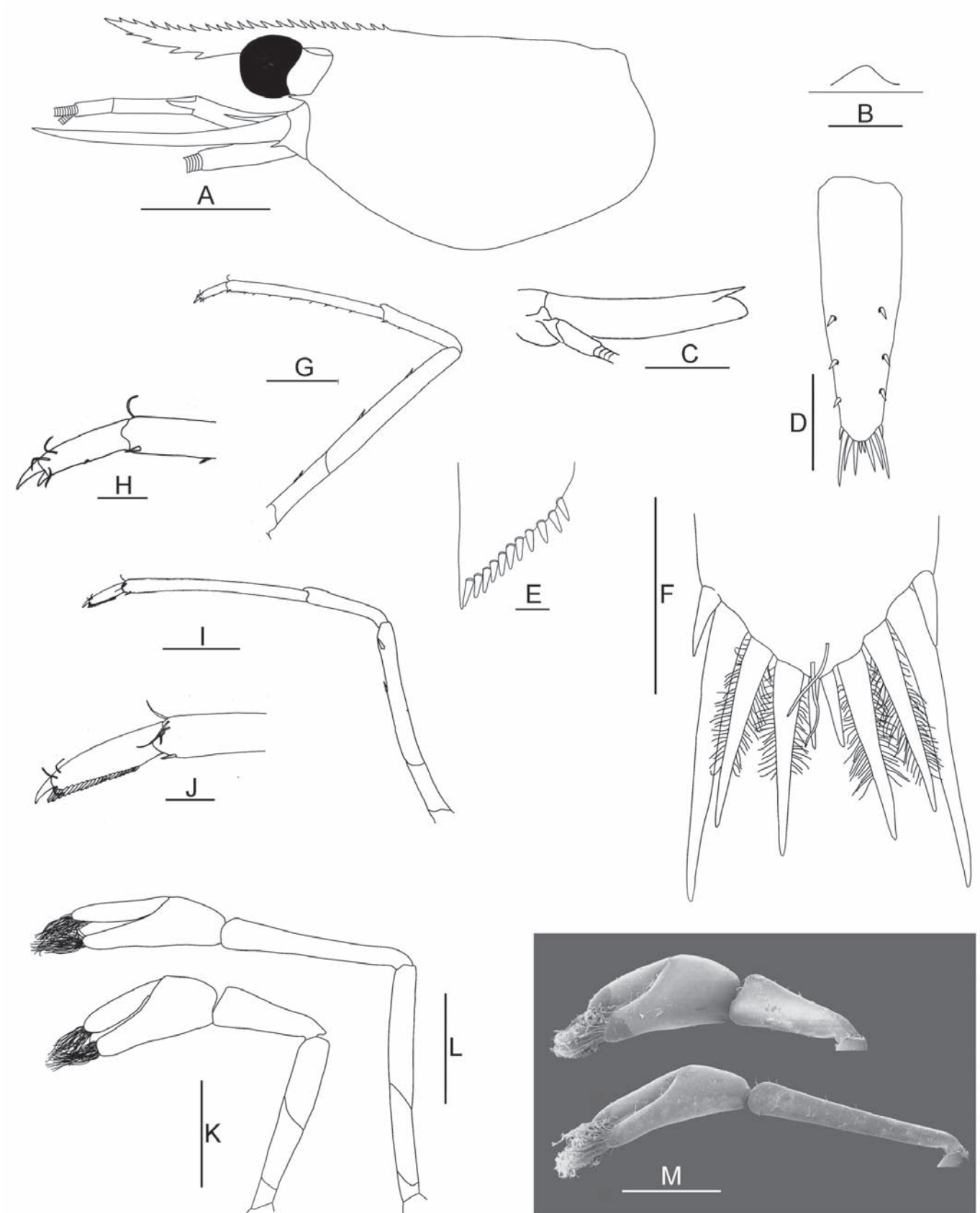


Fig. 37. *Caridina spongicola* from the Malili lake system. A. Cephalothorax and cephalic appendages, female (ZMB 29027); B. Preanal carina; C. Scaphocerite, female (ZMB 29125); D. telson, female (ZMB 29027); E. Uropodal diaeresis; F. Distal end of telson; G. Third pereiopod; H. Dactylus of third pereiopod; I. Fifth pereiopod; J. Dactylus of fifth pereiopod; K. First pereiopod; L. Second pereiopod; M. SEM image of chela and carpus of first and second pereiopods. Scale bars: A, C = 1.0 mm; B, D, F-G, I, K-M = 0.5 mm; E, H, J = 0.1 mm. Figure modified from Zitzler & Cai (2006).

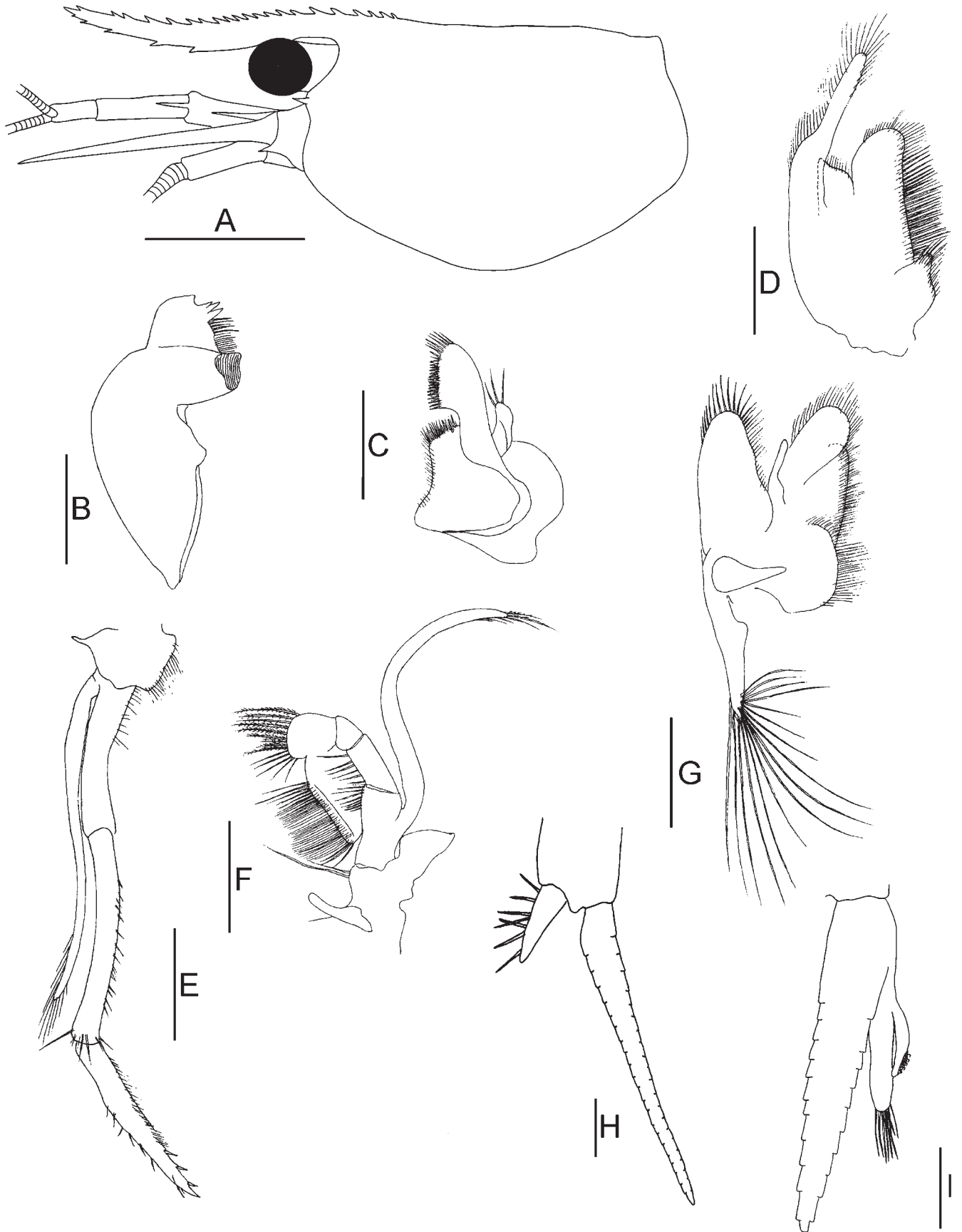


Fig. 38. *Caridina spongicola* from the Malili lake system. A. Cephalothorax and cephalic appendages, female (ZMB 29027); B. Mandible; C. Maxillule; D. First maxilliped; E. Third maxilliped; F. Second maxilliped; G. Maxilla; H. Endopod of male first pleopod (ZMB 29027); I. Appendix masculina of male second pleopod fifth pereopod. Scale bars: A = 1.0 mm; B-G = 0.5 mm; H-I = 0.2 mm. Figure from Zitzler & Cai (2006), i.e. by the same authors.

of 2-5 (-10)m. The shrimps either occur on the sponge or dwell inside its oscula (Zitzler & Cai, 2006; von Rintelen et al., 2007b).

A preliminary gut content analysis was carried out to investigate the shrimp's diet (Zitzler & Cai, 2006). According to these authors, none of the six dissected guts contained traces of poriferean spicules. The spicules are presumably too big (0.2-0.3 mm) to be consumed by the shrimp. On the other hand, a variety of diatoms, which possibly accumulate on or within the sponge, were found in the guts. These findings suggest that the shrimp does not feed on sponge tissue and thus does not parasitize its host. Instead, it appears to be a commensal using the sponge's cavities as shelter and the inherent accumulation of diatoms as a food supply (Zitzler & Cai, 2006).

**Colour pattern.** – Carapace with three transversal dark brown bands (Fig.36C-D), first two usually joined at dorsal surface to form a n-shaped band in lateral view. Anterior part of cephalothorax, antennular peduncle, bases of antennae and posterior rostrum similarly pigmented, whereas anterior rostrum, antennae and distal antennules mostly unpigmented. First and second pereopods white with brown bands, abdomen with a conspicuous white stripe expanding laterally along each side, dorsally densely covered with dark brown bands except for a white patch on third sternum, ventrally uniformly brown. Uropods with a characteristic brown band on distal endopods, endopods and exopods with white-pigmented tips, respectively. Pleopods and telson colourless. Eggs usually dark brown. This colour pattern remains visible even if the shrimp is under stress, the intensity of the colour merely fades (compare Zitzler & Cai, 2006; von Rintelen et al., 2007b). In a few specimens, the colour pattern resembled *C. glaubrechtii*, but the majority was observed to be as mentioned above.

**Taxonomic remarks.** – The rostrum of *C. spongicola* displays a high degree of variation within the populations (Fig. 36B; compare Zitzler & Cai, 2006), similarly to many other species from the Malili lakes. However, certain qualitative characters, i.e. the general shape or the arrangement of the rostral teeth, are constant not only in *C. spongicola*, but in all other ancient lake species (e.g. Schenkel, 1902; Woltereck 1937a, b; Cai & Wowor, 2007).

The colour morph of the majority of living specimens closely resembles *C. woltereckae*, and both species can easily be confused in the field, although *C. woltereckae* is a typical rock dweller and has a much wider distribution. *C. spongicola* is generally smaller (carapace length 1.8-2.8, median 2.4 vs. 2.4-3.8, median 2.8 in *C. woltereckae*) and has a shorter rostrum (reaching to or slightly beyond third segment of antennular peduncle vs. reaching beyond end of scaphocerite in *C. woltereckae*). Its smaller size (cl 1.8-2.8 mm, median 2.4) also distinguishes *C. spongicola* from most of the other lake species apart from *C. loehae* and *C. parvula*. From these, it differs by a longer rostrum (reaching to or slightly beyond third segment of antennular peduncle vs. shorter in the other species), a different shape of the rostrum (more slender and fragile in *C. loehae* and

distinctly stouter in *C. parvula*), and a different number of spines on the dactylus of the fifth pereopod (21-31, median 27 vs. 12-16, median 16 in *C. loehae* vs. 34-39, median 37 in *C. parvula*).

In the molecular phylogeny (Figs. 63-64), *C. spongicola* appears within an unresolved clade of the rock dwellers *C. striata*, *C. glaubrechtii*, and *C. woltereckae* (compare von Rintelen et al., 2007b), although *C. spongicola* differs in morphology and choice of habitat (sponge) from the other species (for example its generally smaller size and a shorter rostrum vs. rostrum reaching beyond end of scaphocerite in the rock dwellers).

### *Caridina striata*, new species

(Figs. 39–41; Table 15)

*Caridina spinata* – von Rintelen et al., 2007b: 262, fig. 2b.

**Material examined.** – Holotype: ovigerous female, cl 3.5 mm (MZB Cru 2121), Indonesia, Sulawesi Selatan, Lake Towuti, north shore, 02°38.56'S, 121°27.82'E, loc. 66-03, on rocks, coll. K. & T. von Rintelen, 26 Sep.2003.

Paratypes (Lake Towuti) – 7 ex. (ZMB 29023, some SEM material), north shore, bay east of Cape Bintu, 02°39.48'S, 121°33.25'E, loc. 68-03, on rocks, coll. K. & T. von Rintelen, 26 Sep.2003; 6 ex. (ZMB 29048, n=6, some SEM material), south shore, approx. 2 km east of Cape Mea, 02°55.8'S, 121°26.92'E, loc. 74-03, on rocks, coll. K. & T. von Rintelen, 28 Sep.2003; 11 ex. (MZB Cru 1815, n=5; ZMB 29095, n=6, some SEM material), Loeha Island, north shore, 02°45.64'S, 121°34.32'E, loc. 97-03, on rocks, coll. K. & T. von Rintelen, 4 Oct.2003; 2 ex. (ZMB 29169, n=2, some SEM material), west shore, north of Cape Wasupute, 02°46.9'S, 121°27.94'E, loc. 78-03, on rocks, coll. K. & T. von Rintelen, 28 Sep.2003; 4 ex. (ZMB 29170, n=4), north shore, west of Cape Manu, 02°41.67'S, 121°36.85'E, loc. 69-03, on boulders in deeper water, coll. K. & T. von Rintelen, 27 Sep.2003; 15 ex. (MZB Cru 1816, n=7; ZMB 29171, n=8), north shore, at cape, 02°39.38'S, 121°29.73'E, loc. 67-03, on rocks in deeper water, coll. K. & T. von Rintelen, 26 Sep.2003; 40 ex. (MZB Cru 1817, n=25; ZMB 29172, n=15), north shore, 02°38.56'S, 121°27.82'E, loc. 66-03, on rocks, coll. K. & T. von Rintelen, 26 Sep.2003; 13 ex. (MZB Cru 1818, n=6; ZMB 29173, n=7), southwest shore, west of Cape Tetetu, 02°54.13'S, 121°23.78'E, loc. 76-03, on rocks, coll. K. & T. von Rintelen, 28 Sep.2003; 13 ex. (MZB Cru 1819, n=6; ZMB 29174, n=7), west shore, south of Cape Timbalo, 02°42.91'S, 121°26.78'E, loc. 94-03, on rocks, coll. K. & T. von Rintelen, 4 Oct.2003; 16 ex. (MZB Cru 1820, n=8; ZMB 29175, n=8), Loeha Island, west shore, 02°45.5'S, 121°31.06'E, loc. 95-03, on rocks, coll. K. & T. von Rintelen, 4 Oct.2003; 9 ex. (MZB Cru 1821, n=4; ZMB 29176, n=5), east shore, 02°52.79'S, 121°31.18'E, loc. 72-03, on rocks, coll. K. & T. von Rintelen, 27 Sep.2003; 7 ex. (ZMB 29177), west shore, at entrance to outlet bay, Cape Larona, 02°48.43'S, 121°24.75'E, loc. 73-03, on rocks, coll. K. & T. von Rintelen, 8 Oct.2003; 4 ex. (ZMB 29178), east shore, south of Cape Tomeraka, 02°44.47'S, 121°37.53'E, loc. 70-03, on rocks, coll. K. & T. von Rintelen, 27 Sep.2003; 9 ex. (ZMB 29299, n=9 and few juveniles, some SEM material), west shore, Cape Bakara, 02°40.771'S, 121°26.11'E, loc. 144-04, on rocks in deeper water, coll. K. & T. von Rintelen, 26 Jul.2004; 1 ex. (ZMB 29337), Loeha Island, southwest shore, 02°45.58'S, 121°31.14'E, loc. 149-04, on rocks in deeper water, coll. K. & T. von Rintelen, 5 Aug.2004; 5 ex. (MZB Cru 1822),

west shore, outlet bay, 02°46.277'S, 121°21.83'E, loc. 02-05, on sponge, coll. K. & T. von Rintelen, 3 Jan.2005.

Paratypes (Lake Mahalona) – 44 ex. (MZB Cru 1823, n=22; ZMB 29039, n=22 and some juveniles, some SEM material), northwest shore, at cape, 02°34.72'S, 121°29.12'E, loc. 56-03, on rocks, coll.

K. & T. von Rintelen, 23 Sep.2003; 5 ex. (ZMB 29102, n=5, some SEM material), east shore, 02°34.217'S, 121°30.681'E, loc. 147-04, on rocks, coll. K. & T. von Rintelen, 3 Aug.2004; 17 ex. (MZB Cru 1824, n=8; ZMB 29298, n=9), north shore, at cape, 02°34.71'S, 121°29.144'E, loc. 148-04, on mixed substrate, coll. K. & T. von Rintelen, 3 Aug.2004.

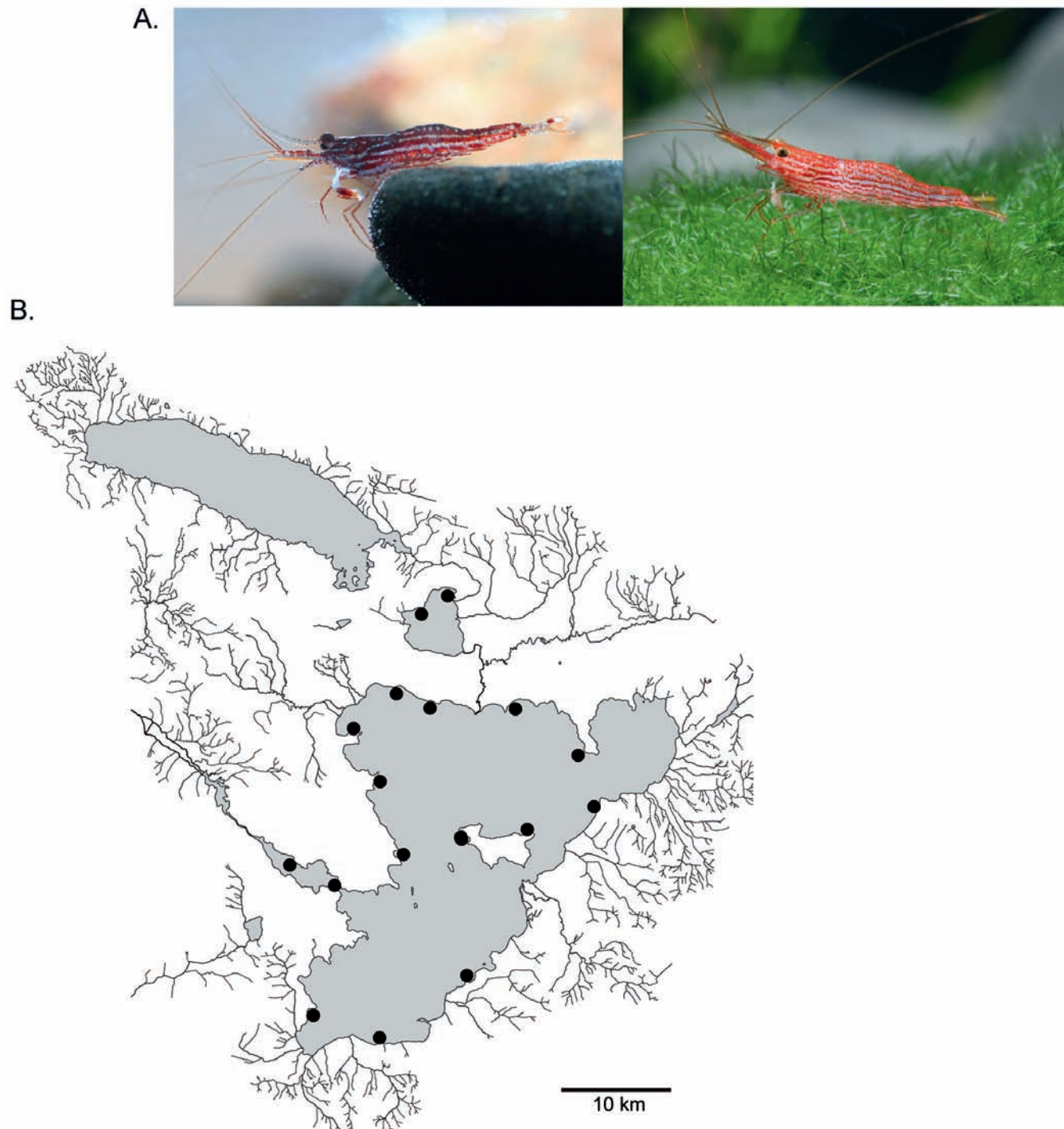


Fig. 39. *Caridina striata* from the Malili lake system. A. Cephalothorax and cephalic appendages, female with short and stout rostrum (ZMB 29048); B. Cephalothorax and cephalic appendages, female with long and slender rostrum (ZMB 29169); C. Rostrum variability (ZMB 29023); D. Uropodal diaeresis, male (ZMB 29023); E. Preanal carina, F. Scaphocerite; G. Telson, female with short and stout rostrum (ZMB 29048); H. Telson, female with long and slender rostrum (ZMB 29169); I. Dactylus of third pereiopod, female (ZMB 29048); J. Dactylus of fifth pereiopod; K. Distal end of telson (ZMB 29048); L. Distal end of telson (ZMB 29169); M. Third pereiopod, female (ZMB 29048); N. Fifth pereiopod; O. Endopod of male first pleopod (ZMB 29023); P. Appendix masculina of male second pleopod; Q. First pereiopod, female (ZMB 29048); R. Second pereiopod; S. SEM image of chela and carpus of first and second pereiopods, female (ZMB 29095). Scale bars: A-C, F = 1.0 mm; E, G-H, M-S = 0.5 mm; D, I-L = 0.1 mm.

Table 15. Summary of standard morphometric parameters for *Caridina striata*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	1.7-3.8	3.0 $\pm$ 0.5	3.1	36
rl / cl	0.8-2.4	1.3 $\pm$ 0.4	1.1	36
n dorsal rostral teeth	3-25	12 $\pm$ 8	15	36
n ventral rostral teeth	4-28	9 $\pm$ 6	7	36
abds6 / cl	0.5-0.8	0.6 $\pm$ 0.1	0.6	36
abds6 / abds5	1.4-2.1	1.7 $\pm$ 0.2	1.7	20
abds6 / h tel	0.8-1.1	1.0 $\pm$ 0.1	1.0	14
h tel / w tel	2.9-3.7	3.4 $\pm$ 0.4	3.4	5
n spines uropodal diaeresis	11-14	13 $\pm$ 1	13	5
h ch1 / w ch1	2.2-3.0	2.4 $\pm$ 0.2	2.4	21
h ch1 / h ca1	1.1-1.3	1.2 $\pm$ 0.1	1.2	35
h ca1 / w ca1	2.5-3.5	2.9 $\pm$ 0.3	2.8	21
h ch2 / w ch2	2.7-4.0	3.1 $\pm$ 0.3	3.0	22
h ch2 / h ca2	0.7-1.0	0.7 $\pm$ 0.1	0.7	20
h ca2 / w ca2	5.5-7.5	6.3 $\pm$ 0.5	6.1	21
n spines p3	2-3	3 $\pm$ 0	3	5
n spines p5	24-35	31 $\pm$ 5	33	5

**Description.** – Carapace length 1.7-3.8 mm (n=36). Rostrum (Fig. 40A-C; Table 15) generally long to very long, anterior upturned, reaching beyond end of scaphocerite; rostrum dimorphic, either very long and slender, reaching far beyond end of scaphocerite (Fig. 40B) or shorter and broader with less teeth, reaching beyond end of scaphocerite (Fig. 40A); 0.8-2.4 times as long as carapace (n=36), armed dorsally with 3-25 teeth (including 3-5 teeth posterior to orbital margin), anterior less densely spaced, armed ventrally with 4-28 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.6 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 1.0-1.1 times as long as carapace (n=5), second segment 1.8-2.8 times length of third segment, third segment 0.2-0.4 times length of basal segment. Stylocerite reaching 0.9-1.1 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 40F) 5.0-5.7 times as long as wide (n=5).

Sixth abdominal somite 0.5-0.8 times length of carapace (n=36), 1.4-2.1 times as long as fifth somite (n=20), 0.8-1.1 times length of telson (n=14). Telson (Fig. 40G-H, K-L) 2.9-3.7 times as long as wide (n=5), distal margin rounded, without projection, with 3-4 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 4 pairs of spines, lateral pair distinctly longer than intermediate pairs, median pair not always shortest. Preanal carina (Fig. 40E) rounded, without a spine. Uropodal diaeresis (Fig. 40D) with 11-14 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipod present on first pereopod. Incisor process of mandible (Fig. 41A) ending in a row of 3-4 small

teeth, molar process truncated. Lower lacinia of maxillula (Fig. 41B) broadly rounded, upper lacinia elongated, with numerous distinct teeth and setae on inner margin, palp slender. Upper endites of maxilla (Fig. 41C) subdivided, palp short, scaphognathite tapering posteriorly with numerous long, curved setae at posterior end. Distal end of palp of first maxilliped (Fig. 41F) triangular, with a finger-like projection; flagellum of the exopod very elongated, endopod high, reaching half the flagellum of exopod in length. Second maxilliped (Fig. 41E) typical. Third maxilliped (Fig. 41D) with ultimate segment distinctly shorter than penultimate segment.

Chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig. 40Q-S); chela of first pereopod 2.2-3.0 times as long as wide (n=21), 1.1-1.3 times length of carpus (n=35); tips of fingers rounded, without hooks; dactylus 1.0-1.3 times as long as palm (n=7); carpus 2.5-3.5 times as long as wide (n=21), 1.2-1.4 times length of merus (n=5). Chela of second pereopod 2.7-4.0 times as long as wide (n=22), 0.7-1.0 times length of carpus (n=20); tips of fingers rounded, without hooks, dactylus 1.1-1.4 times as long as palm (n=7); carpus 5.5-7.5 times as long as wide (n=21), 1.3-1.5 times as long as merus (n=5).

Third pereopod (Fig. 40I,M) slender, dactylus 4.4-5.4 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 2-3 accessory spines on flexor margin; propodus 11.8-12.7 times as long as wide, 3.1-3.6 times as long as dactylus; carpus 5.2-6.6 times as long as wide, 0.6-0.7 times as long as propodus, 0.5 times as long as merus; merus 8.9-9.7 times as long as wide, bearing 3-4 strong, movable spines on posterior margin of outer surface.

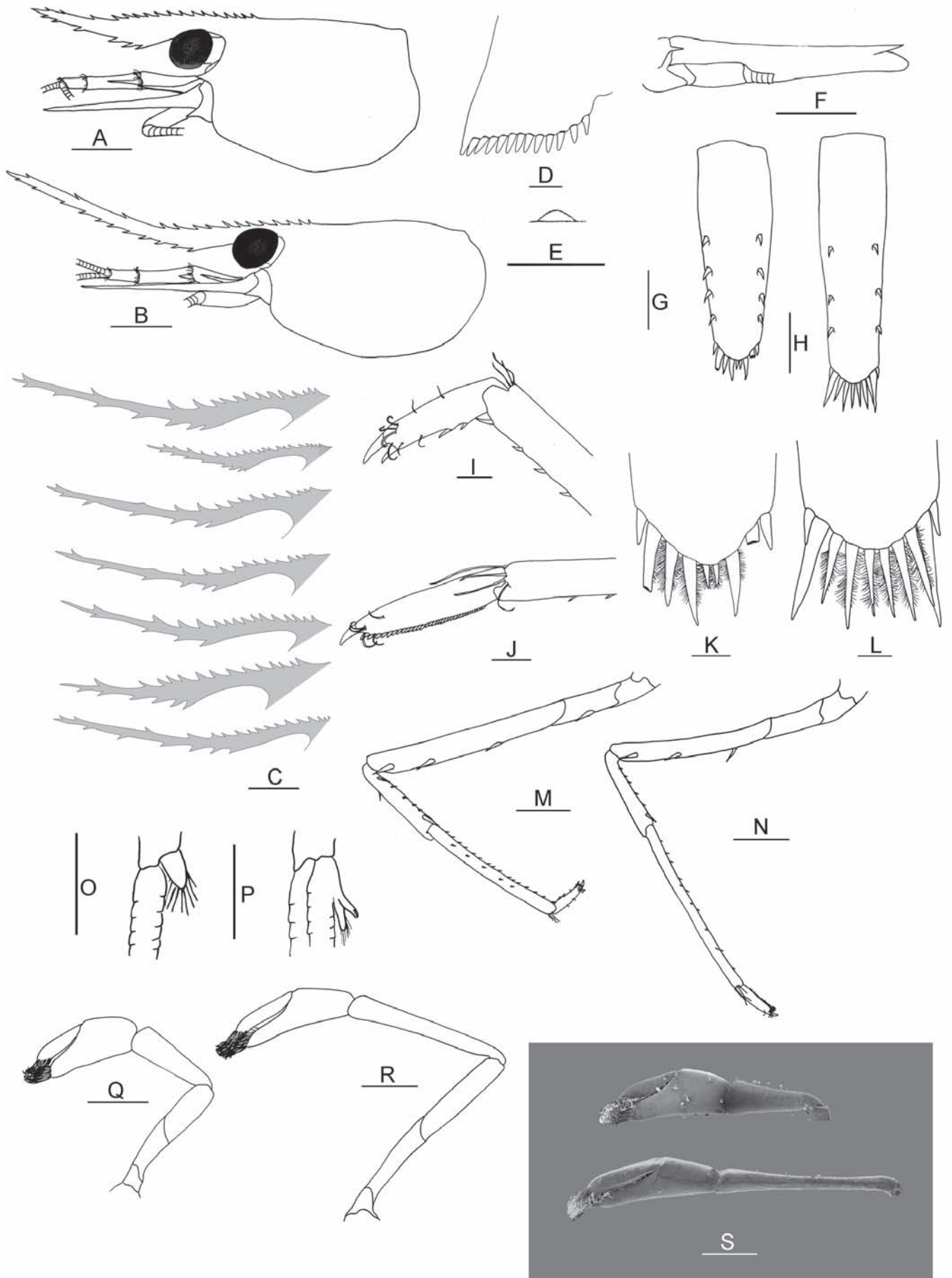


Fig. 40. *Caridina striata* from the Malili lake system. A. Colour pattern of living animals (not to scale). B. Distribution. Picture on the right courtesy of Chris Lukhaup.

Fifth pereiopod slender (Fig. 40J,N), dactylus 4.4-6.0 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 24-35 accessory spines on flexor margin; propodus 13.1-17.6 times as long as wide, 3.1-4.2 times as long as dactylus; carpus 5.0-6.4 times as long as wide, 0.5 times as long as propodus, 0.5-0.6 times as long as merus; merus 9.1-9.7 times as long as wide, bearing 3-4 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 40O) elongated triangular, 1.6-2.1 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 40P) 0.8-1.0 times length of appendix masculina (n=5).

Ovigerous females with 17-38 eggs (n=3 females); egg size 0.8-0.9 x 0.5 mm (n=37, eggs with and without eyes).

**Distribution.** – *C. striata* is endemic to the Malili lake system. There, widely distributed and often numerous in Lake Towuti, but was also found in Lake Mahalona (Fig. 39B).

**Biology and ecology.** – *C. striata* is a hard substrate dweller on rocks. It occurs both in shallow water regions on and under smaller rocks, and in deeper water zones (below 3 m) between larger rocks (boulders). When disturbed, it tries to escape side- or downwards rather than in other directions. *C. striata* is often found in syntopy with other rock dwellers in Lake Towuti, such as *C. profundicola* and *C. spinata*, but particularly *C. glaubrechtii* and *C. woltereckae*.

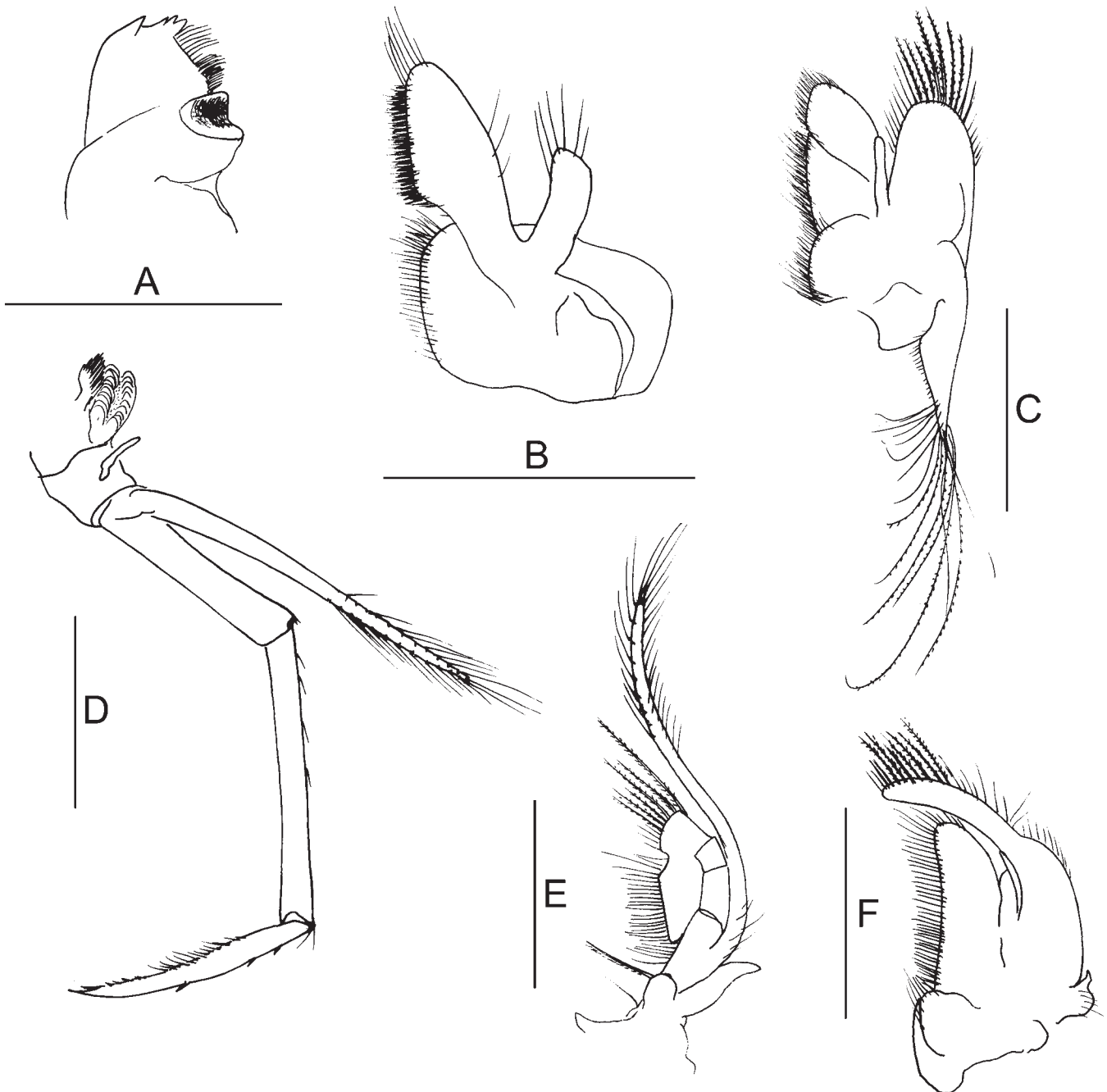


Fig. 41. *Caridina striata* from the Malili lake system. A. Mandible (ZMB 29172); B. Maxillula; C. Maxilla; D. third maxilliped; E. second maxilliped; F. first maxilliped. Scale bars: A-F = 1mm.



**Colour pattern.** – Body red, laterally with characteristic white stripes, dorsally with some white spots (Fig. 39A). The uropods sometimes bear red and white patches on the distal margin. Appendages either transparent or reddish-transparent. First and second pereopod usually conspicuously white. When animals are feeding, the white chelipeds were observed to be always clearly visible, whereas the rest of the (darker coloured) body was more or less camouflaged. This colour pattern remains visible even if the shrimp is under stress, the intensity of the colour merely fades.

**Etymology.** – The name *Caridina striata*, new species, refers to the characteristic colour pattern of red and white stripes (the Latin word *striatus* means striped).

**Taxonomic remarks.** – As alcohol bleached material, *C. striata* is almost identical with *C. glaubrechti* and *C. woltereckae*, although the colour pattern in living animals allows an unambiguous separation. It slightly differs from *C. woltereckae* by a higher number of spines on the dactylus of the fifth pereopod (24–35, median 33 vs. 13–22, median 20 in *C. woltereckae*). The dimorphic character of the rostrum in *C. striata* was not observed in the other two species.

In the molecular phylogeny (Figs. 63–64), all three species form a single clade with the sponge dweller *C. spongicola*, but their relationship is not resolved within this clade (compare von Rintelen et al., 2007b, in review). However,

the distinct colour patterns in all three species were found to be stable over the years of sampling. While morphological differences are largely lacking, they differ in behaviour and distribution (compare von Rintelen et al., 2007b, in review). *C. striata* was observed to be generally more active and faster than the other two rock dwellers and usually tried to escape sideways instead of staying attached to a rock as observed in *C. glaubrechti* and *C. woltereckae*. *C. striata* also occurs in Lake Mahalona, whereas the others seem to be restricted to Lake Towuti.

***Caridina tenuirostris* Woltereck, 1937a**  
(Figs. 42–45; Table 16)

*Caridina tenuirostris* Woltereck, 1937a: 224, fig. I.8, pls. 3,6 (type locality: Lake Towuti at Lingkona).

*Caridina tenuirostris* – Woltereck, 1937b: 309, fig. 12; Chace 1997: 20; von Rintelen et al., 2008: 2244, Table 1.

*Cardina tenuirostris* – Brooks, 1950: 168 (erroneous spelling).

*Caridina Towutensis* – Woltereck, 1937a: 220, fig. I.2, pls. 3,6 (type locality: Lake Towuti, South).

*Caridina towutensis* – Woltereck, 1937b: 301, fig. 7 (type locality further specified as Lake Towuti, South, Cape Sirioga); Chace, 1997: 20; von Rintelen et al., 2008: 2244, Table 1.

*Cardina towutensis* – Brooks, 1950: 168 (erroneous spelling).

**Material examined.** – Neotype: ovigerous female (cl. 2.8 mm), Lake Towuti, southwest shore, west of Cape Tetetu, 02°54.13'S,

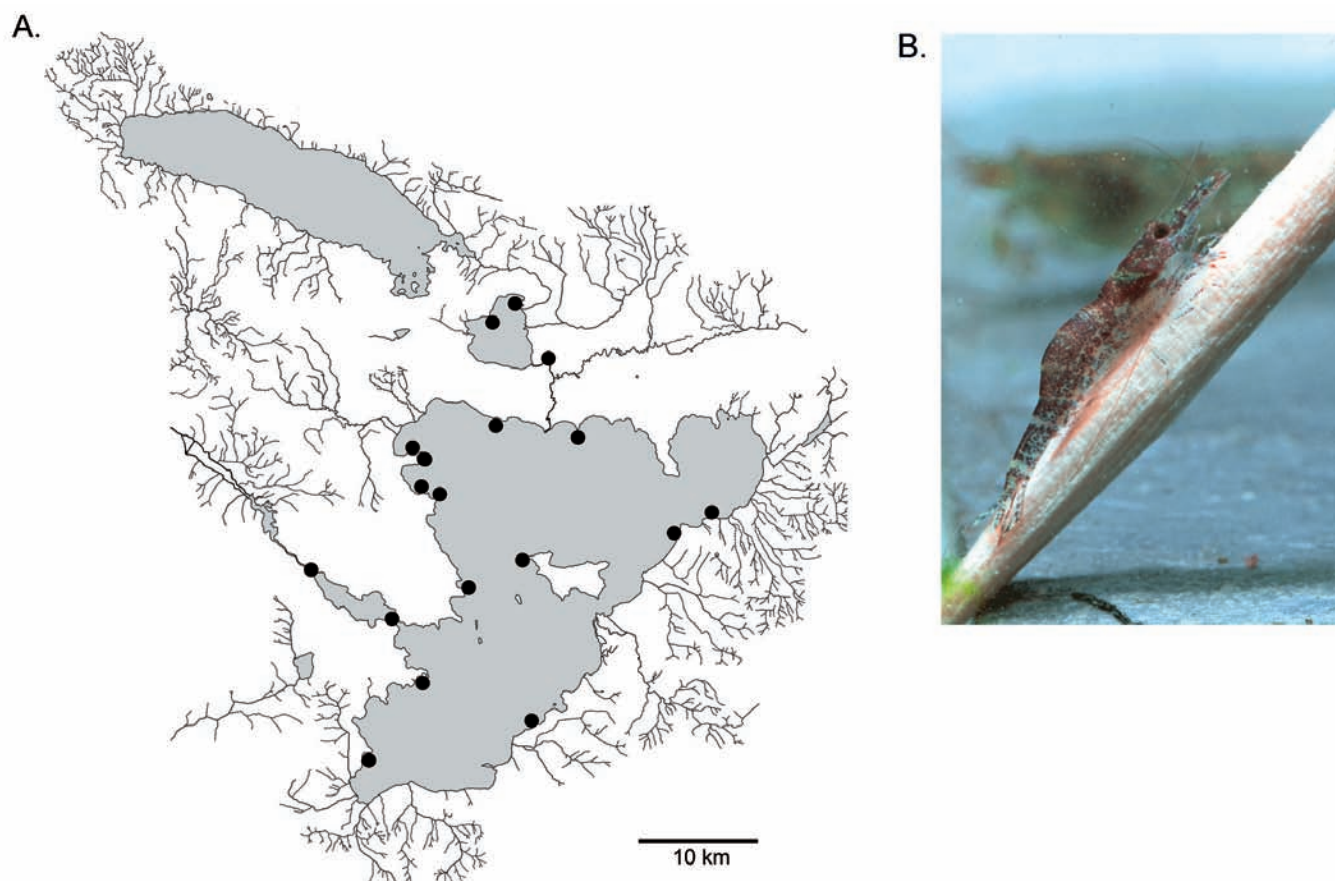


Fig. 42. *Caridina tenuirostris* from the Malili lake system. A. Distribution. B. Colour pattern of living animal (not to scale). Picture courtesy of Rainer Masche.

Table 16. Summary of standard morphometric parameters for *Caridina tenuirostris*.

parameter	range	mean ± SD	median	n
cl (mm)	2.4-3.3	2.9 ± 0.2	2.9	32
rl / cl	1.1-1.8	1.5 ± 0.2	1.4	32
n dorsal rostral teeth	9-18	14 ± 2	14	32
n ventral rostral teeth	10-24	14 ± 3	15	32
abds6 / cl	0.6-0.9	0.8 ± 0.0	0.8	32
abds6 / abds5	1.8-2.3	2.0 ± 0.1	1.9	20
abds6 / h tel	1.0-1.5	1.2 ± 0.1	1.3	12
h tel / w tel	2.8-5.7	3.6 ± 1.2	3.4	5
n spines uropodal diaeresis	7-8	8 ± 0	8	5
h ch1 / w ch1	1.7-2.3	1.9 ± 0.2	1.9	20
h ch1 / h ca1	1.3-1.7	1.5 ± 0.1	1.5	32
h ca1 / w ca1	1.5-2.4	1.8 ± 0.2	1.8	20
h ch2 / w ch2	1.9-3.1	2.4 ± 0.4	2.3	20
h ch2 / h ca2	0.8-1.0	0.9 ± 0.1	0.9	32
h ca2 / w ca2	3.1-5.0	4.0 ± 0.7	3.8	20
n spines p3	3	-	-	6
n spines p5	11-15	13 ± 1.7	14	6

121°23.78'E, loc. 76-03, on wood (MZB Cru 2126), coll. K. & T. von Rintelen, 28 Sep.2003.

Others (Lake Towuti) – 32 ex. (MZB Cru 1782, n=17; ZMB 29034, n=15, some SEM material), east shore, south of Cape Tomeraka, 02°44.47'S, 121°37.53'E, loc. 70-03, on wood, coll. K. & T. von Rintelen, 27 Sep.2003; 27 ex. (MZB Cru 1783, n=15; ZMB 29043, n=12), wet shore, at entrance to outlet bay, Cape Larona, 02°48.43'S, 121°24.75'E, loc. 73-03, on wood, coll. K. & T. von Rintelen, 27 Sep.2003; 30 ex. (MZB Cru 1784, n=15; ZMB 29122, n=15), north shore, bay east of Cape Bintu, 02°39.48'S, 121°33.25'E, loc. 68-03, on wood, coll. K. & T. von Rintelen, 26 Sep.2003; 10 ex. (ZMB 29123), east shore, 02°52.79'S, 121°31.18'E, loc. 72-03, on wood, coll. K. & T. von Rintelen, 27 Sep.2003; 12 ex. (ZMB 29124), Loeha Island, west shore, 02°45.5'S, 121°31.06'E, loc. 95-03, on wood, coll. K. & T. von Rintelen, 4 Oct.2003; 35 ex. (MZB Cru 1785, n=12; ZMB 29127, n=23, some SEM material), north shore, at cape, 02°29.73'S, 121°29.73'E, loc. 67-03, on wood, coll. K. & T. von Rintelen, 26 Sep.2003; 6 ex. (ZMB 29132), southwest shore, Cape Sioloya, 02°50.7'S, 121°26.32'E, loc. 77-03, on wood, coll. K. & T. von Rintelen, 28 Sep.2003; 34 ex. (MZB Cru 1786, n=20; ZMB 29133, n=14), southwest shore, west of Cape Tetetu, 02°54.13'S, 121°23.78'E, loc. 76-03, on wood, coll. K. & T. von Rintelen, 28 Sep.2003; 6 ex. (ZMB 29134), west shore, north of Cape Wasupute, 02°46.9'S, 121°27.94'E, loc. 78-03, on wood, coll. K. & T. von Rintelen, 28 Sep.2003; 26 ex. (MZB Cru 1787, n=9; ZMB 29300, n=17), east shore, 02°43.82'S, 121°39.211'E, loc. 115-04, on wood, coll. K. & T. von Rintelen, 28 Jul.2004; 3 ex. (ZMB 29311), west shore, west of Cape Timbalo, 02°42.631'S, 121°26.389'E, loc. 145-04, on mixed substrate with wood, coll. K. & T. von Rintelen, 26 Jul.2004; 7 ex. (MZB Cru 1788, n=4; ZMB 29312, n=3), west shore, Cape Bakara, 02°40.771'S, 121°26.11'E, loc. 144-04, on mixed substrate with wood, coll. K. & T. von Rintelen, 26 Jul.2004; 3 ex. (ZMB 29450), west shore, Cape Bakara, 02°40.876'S, 121°26.043'E, loc. 225-05, on wood, coll. K. & T. von Rintelen, 23 Oct.2005; 13 ex. (ZMB 29130, n=13 and some juveniles, some SEM material), Larona River, close to outlet bay, 02°45.8'S, 121°20.8'E, loc. 51-03, on wood, coll. K. & T. von Rintelen, 21 Sep.2003.

Others (Lake Mahalona) – 47 ex. (MZB Cru 1789, n=23 and some juveniles; ZMB 29040, n=24, some SEM material), northwest shore, at cape, 02°34.72'S, 121°29.12'E, loc. 56-03, on wood, coll. K. & T. von Rintelen, 23 Sep.2003; 3 ex. (ZMB 29224), east shore, 02°34.217'S, 121°30.681'E, loc. 147-04, on wood, coll. K. & T. von Rintelen, 3 Aug.2004; 6 ex. (ZMB 29071), Tominanga River, approx. 2.2 km north of Lake Towuti, 02°36.5'S, 121°31.78'E, loc. 58-03, on wood, coll. K. & T. von Rintelen, 23 Sep.2003.

**Description.** – Carapace length 2.4-3.3 mm (n=32). Rostrum (Fig. 43A-B; Table 16) long and throughout slender, reaching far beyond end of scaphocerite, 1.1-1.8 times as long as carapace (n=32), armed dorsally with 9-18 teeth (including 1-4 teeth posterior to orbital margin), approx. anterior 2/3 to ½ unarmed, without subapical teeth, armed ventrally with 10-24 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.6-0.7 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.9-1.0 times as long as carapace (n=5), second segment 1.9-2.2 times length of third segment, third segment 0.3 times length of basal segment. Stylocerite reaching 0.8-0.9 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 43F) 4.3-5.4 times as long as wide (n=5).

Sixth abdominal somite 0.6-0.9 times length of carapace (n=32), 1.8-2.3 times as long as fifth somite (n=20), 1.0-1.5 times length of telson (n=12). Telson (Fig. 43E,K) 2.8-5.7 times as long as wide (n=5), distal margin rounded, without projection, with 3-4 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 3-5 pairs of spines, lateral pair distinctly longer than intermediate pairs, median pair shortest. Preanal carina (Fig. 43C) with a spine. Uropodal diaeresis (Fig. 43D) with 7-8 movable spinules (n=5).

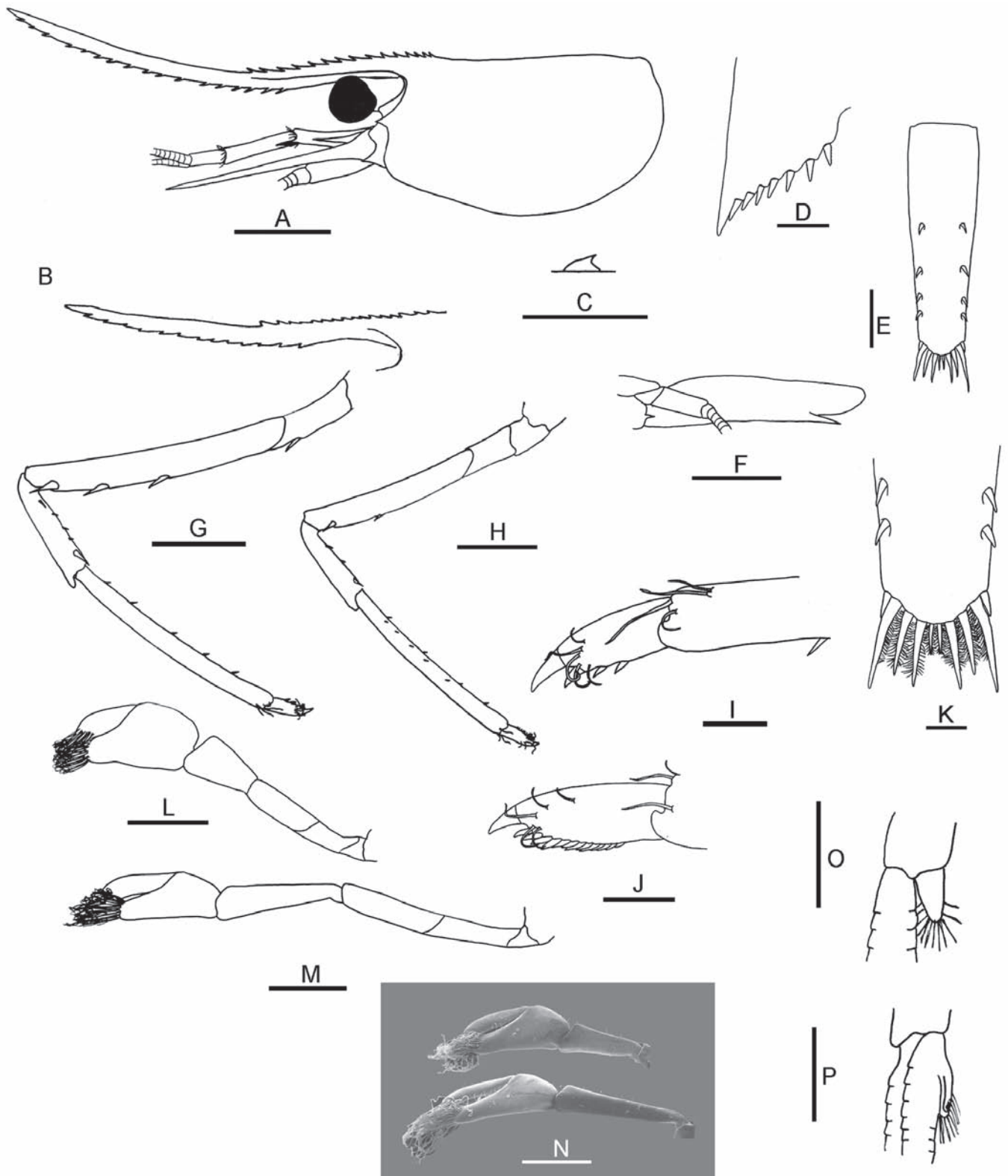


Fig. 43. *Caridina tenuirostris* from the Malili lake system. A. Cephalothorax and cephalic appendages, male (ZMB 29127); B. Woltereck's drawing of the rostrum (modified from 1937a); C. Preanal carina, male (ZMB 29127); D. Uropodal diaeresis; E. Telson, female (ZMB 29127); F. Scaphocerite, male (ZMB 29127); G. Third pereiopod; H. Fifth pereiopod; I. Dactylus of third pereiopod; J. Dactylus of fifth pereiopod; K. Distal end of telson, female (ZMB 29127); L. First pereiopod, male (ZMB 29127); M. Second pereiopod; N. SEM image of chela and carpus of first and second pereiopods, female (ZMB 29071); O. Endopod of male first pleopod (ZMB 29127); P. Appendix masculina of male second pleopod. Scale bars: A, F = 1.0 mm; C, E, G-H, L-P = 0.5 mm; D, I-K = 0.1 mm; B = no scale available.

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereiopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipod on first pereiopod. Incisor process of mandible (Fig. 44A) ending in a row of 3-4 small teeth, molar process truncated. Lower lacinia of maxillula (Fig. 44B) broadly rounded, upper lacinia elongate, with numerous distinct teeth and setae on inner margin, palp slender. Upper endites of maxilla (Fig. 44C) subdivided, palp elongated, scaphognathite broadly tapering posteriorly with numerous long, curved setae at posterior end. Distal end of palp of first maxilliped (Fig. 44F) triangular, ending with a finger-like projection; flagellum of the exopod short, endopod high, not exceed the flagellum of exopod in length. Second maxilliped (Fig. 44E) typical. Third maxilliped (Fig. 44D) ultimate segment slightly shorter than penultimate segment.

Chela and carpus of first pereiopod distinctly stouter and broader than chela and carpus of second pereiopod (Fig. 43L-N); chela of first pereiopod 1.7-2.3 times as long as wide (n=20), 1.3-1.7 times length of carpus (n=32); tips of fingers rounded, without hooks; dactylus 1.0-1.6 times as long as palm (n=5); carpus 1.5-2.4 times as long as wide (n=20), 1.0-1.6 times length of merus (n=5). Chela of second pereiopod 1.9-3.1 times as long as wide (n=20), 0.8-1.0 times length of carpus (n=32); tips of fingers rounded, without hooks, dactylus 1.5-1.7 times as long as palm (n=5); carpus 3.1-5.0 times as long as wide (n=20), 1.1-1.3 times as long as merus (n=5).

Third pereiopod (Fig. 43G,I) slender, dactylus 2.0-3.2 times as long as wide (terminal spine included, without spines of flexor margin; n=6), terminating in one large claw with 3 accessory spines on flexor margin; propodus 8.6-12.2 times

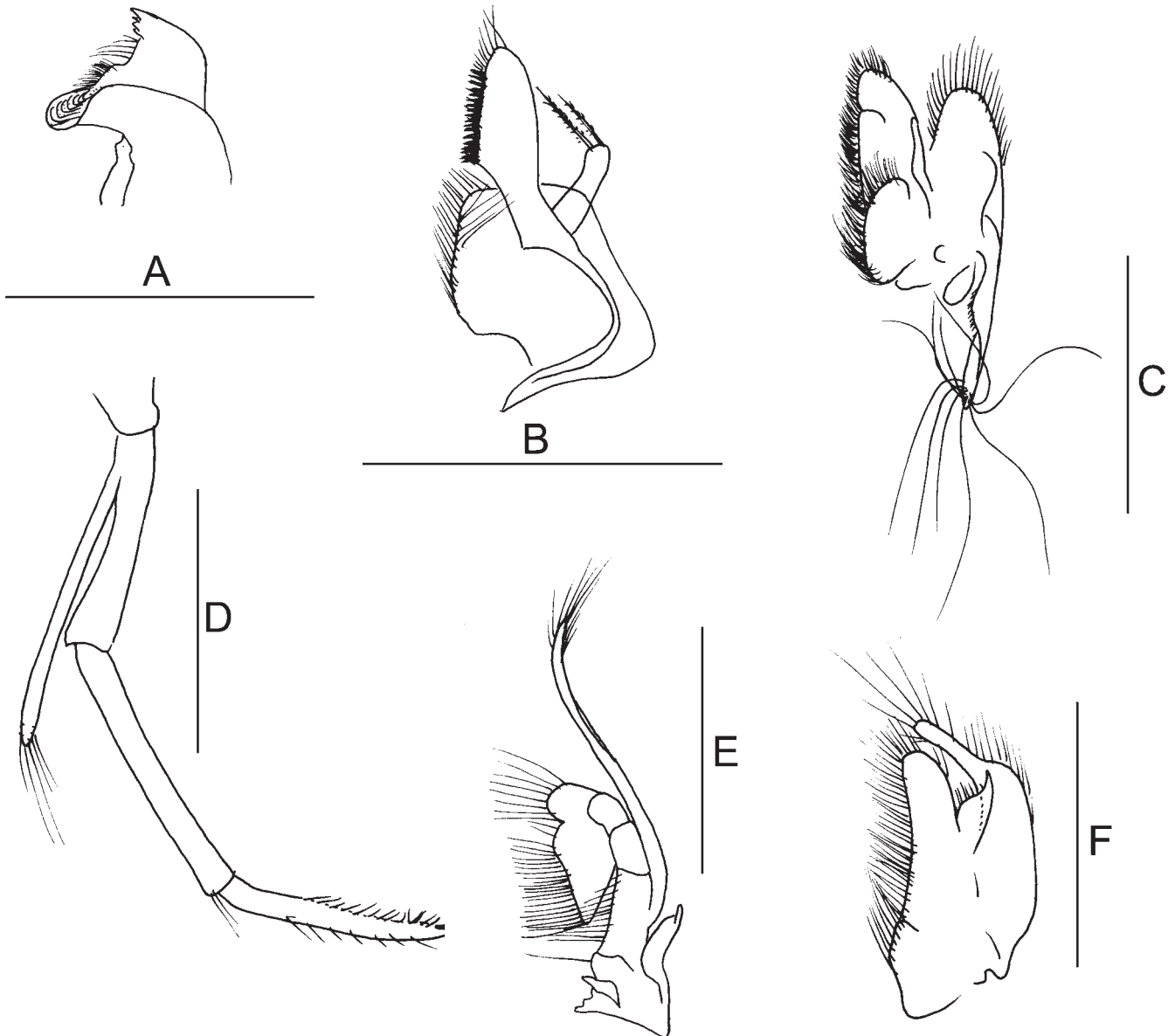


Fig. 44. *Caridina tenuirostris* from the Malili lake system. A. Mandible (ZMB 29133); B. Maxillula; C. Maxilla; D. third maxilliped; E. second maxilliped; F. first maxilliped. Scale bars: A-F = 1mm.

as long as wide, 4.3-6.8 times as long as dactylus; carpus 3.6-5.2 times as long as wide, 0.5-0.6 times as long as propodus, 0.5 times as long as merus; merus 6.8-8.3 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Fifth pereiopod slender (Fig. 43H,J), dactylus 2.5-3.3 times as long as wide (terminal spine included, without spines of flexor margin; n=6), terminating in one large claw with 11-15 accessory spines on flexor margin; propodus 10.5-14.4

times as long as wide, 4.8-6.4 times as long as dactylus; carpus 3.9-4.6 times as long as wide, 0.5-0.6 times as long as propodus, 0.6 times as long as merus; merus 6.1-7.3 times as long as wide, bearing 2 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 43O) elongated triangular, 1.6-2.3 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 26P) 0.9-1.0 times as long as appendix masculina (n=5).

A.

B.

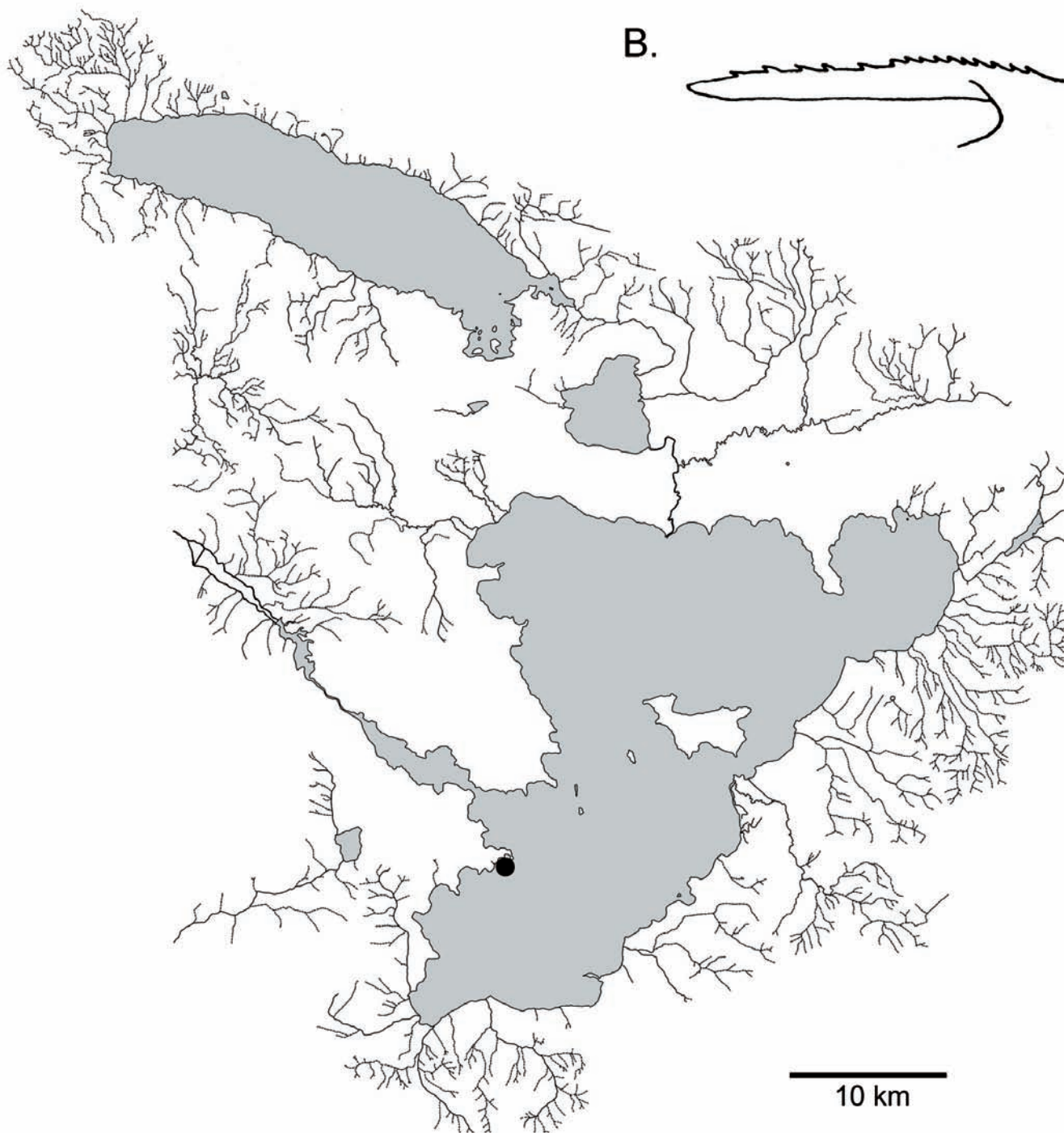


Fig. 45. *Caridina towutensis* sensu Woltereck (1937a, b). A. The presumed type locality in Lake Towuti. B. Woltereck's drawing of the rostrum (modified from 1937a).

Ovigerous females with 11-22 eggs (n=3 females); egg size 0.8-0.9 x 0.5-0.6 mm (n=51, eggs with and without eyes).

**Distribution.** – *C. tenuirostris* is endemic to the Malili lake system. It occurs in Lake Towuti, Lake Mahalona, and the connecting Tominanga River as well as Larona River close to the outlet bay of Lake Towuti (Fig. 42A; for locality names see Fig. 1.C).

**Biology and ecology.** – With its rather stout first and second pereopods, *C. tenuirostris* represents a typical hard-substrate dweller. The majority of specimens were collected from wood. It often occurs syntopically on wood with *C. lanceolata* in Lake Towuti and Lake Mahalona, but whereas *C. lanceolata* occurs on various substrates, the occurrence of *C. tenuirostris* is mainly restricted to wood.

**Colour pattern.** – The primary colour of *C. tenuirostris* is brown with several white transversal stripes all over the body (Fig. 42B). A conspicuous white band is visible at the distal part of the abdomen. Appendages are transparent or partly brownish. This colour pattern remains visible even if the shrimp is under stress, though the intensity of the colour merely fades.

**Taxonomic remarks.** – The arrangement of rostral teeth slightly resembles that in *C. lanceolata*, but *C. tenuirostris* has a distinctly more slender rostrum, a higher number of ventral teeth (10-24, median 15 vs. 4-13, median 7 in *C. lanceolata*), always lacking subapical teeth, and a shorter sixth abdominal somite compared to carapace length (0.6-0.9, median 0.8 vs. 0.8-1.1, median 1.0 in *C. lanceolata*). The pereopods are further distinctively stouter than in *C. lanceolata*. The colour pattern of *C. tenuirostris* closely resembles *C. glaubrechti*, but both species not only differ in their substrate preference (wood vs. rocks in *C. glaubrechti*), but by the continuous dorsal denticulation of the rostrum (vs. anterior dorsal part always completely unarmed in *C. tenuirostris*), a different number of spines on the uropodal diaeresis (7-8, median 8 vs. 11-14, median 12 in *C. glaubrechti*), and on the dactylus of the fifth pereopod (11-15, median 14 vs. 14-35, median 28 in *C. glaubrechti*).

In the molecular phylogeny (Figs. 63-64), *C. tenuirostris* is genetically distinct from all other ancient lake species.

Woltereck's (1937a) species *C. towutensis* was never reported by any later collectors, e.g. neither by M. Kottelat nor C. Schubart (see Cai et al., 2009), and was not found during fieldwork for this study at the Malili lakes including an exhaustive search at the (presumed) type locality at Cape Sirioga [Sioloya], Lake Towuti, in 2005 (Fig. 45A; Yixiong Cai, K. & T. von Rintelen, pers. field observation). However, at this locality (loc. 77-03) other species were found, i.e. *C. lanceolata*, *C. parvula*, *C. masapi*, and *C. tenuirostris*. A possible explanation could be the extinction of this tiny species ("total length of largest specimen including the rostrum 16 mm"; Woltereck, 1937b: 301), but this seems unlikely for no other species has become extinct since

Woltereck's descriptions. A rather more plausible explanation is the misinterpretation of *C. towutensis* as a distinct species. Woltereck examined only nine specimens and might have incidentally described local variations of another species. Woltereck's drawing of the rostrum (Fig. 45B) closely resembles juveniles or small adults (usually males) of *C. tenuirostris*, that have not developed full rostrum length yet. Consequently, we here synonymize *C. towutensis* with *C. tenuirostris*.

### *Caridina woltereckae* Cai, Wowor & Choy, 2009

(Figs. 46–47; Table 17)

*Caridina woltereckae* Cai et al., 2009: 19, Fig. 3 (type locality: Lake Towuti, Cape Larona, near Sungai [River] Larona outlet, rocky coast with white sand substrate).

*Caridina* sp.2 – von Rintelen et al., 2007b: 262, fig. 2b.

**Material examined.** – Lake Towuti: 28 ex. (MZB Cru 1828, n=10 and few juveniles; ZMB 29037, n=18, some SEM material), west shore, at entrance to outlet bay, Cape Larona, 02°48.43'S, 121°24.75'E, loc. 73-03, (MZB) on mixed substrate, (ZMB) on rocks, coll. K. & T. von Rintelen, 8 Oct.2003; 24 ex. (MZB Cru 1829, n=12; ZMB 29044, n=12, some SEM material), north shore, bay east of Cape Bintu, 02°39.48'S, 121°33.25'E, loc. 68-03, on rocks, coll. K. & T. von Rintelen, 26 Sep.2003; 13 ex. (MZB Cru 1830, n=6; ZMB 29052, n=7, some SEM material), Loeha Island, west shore, 02°45.5'S, 121°31.06'E, loc. 95-03, on rocks, coll. K. & T. von Rintelen, 4 Oct.2003; 13 ex. (MZB Cru 1831, n=7; ZMB 29106, n=6, some SEM material), southwest shore, west of Cape Tetetu, 02°54.13'S, 121°23.78'E, loc. 76-03, on rocks, coll. K. & T. von Rintelen, 28 Sep.2003; 4 ex. (ZMB 29144), west shore, south of Cape Timbalo, 02°42.91'S, 121°26.78'E, loc. 94-03, on rocks, coll. K. & T. von Rintelen, 4 Oct.2003; 7 ex. (ZMB 29145), Loeha Island, north shore, 02°45.64'S, 121°34.32'E, loc. 97-03, on rocks, coll. K. & T. von Rintelen, 4 Oct.2003; 21 ex. (MZB Cru 1832, n=9; ZMB 29146, n=12), north shore, 02°38.56'S, 121°27.82'E, loc. 66-03, on rocks, coll. K. & T. von Rintelen, 26 Sep.2003; 13 ex. (MZB Cru 1833, n=6; ZMB 29147, n=7, some SEM material), north shore, at cape, 02°39.38'S, 121°29.73'E, loc. 67-03, on rocks in deeper water, coll. K. & T. von Rintelen, 26 Sep.2003; 2 ex. (ZMB 29148, n=2 and few juveniles, some SEM material), north shore, west of Cape Manu, 02°41.67'S, 121°36.85'E, loc. 69-03, on rocks in deeper water, coll. K. & T. von Rintelen, 27 Sep.2003; 1 ex. (ZMB 29149, n=1 and few juveniles), west shore, north of Cape Wasupute, 02°46.9'S, 121°27.94'E, loc. 78-03, on rocks, coll. K. & T. von Rintelen, 28 Sep.2003; 3 ex. (ZMB 29151), east shore, south of Cape Tomeraka, 02°44.47'S, 121°37.53'E, loc. 70-03, on rocks, coll. K. & T. von Rintelen, 27 Sep.2003; 1 ex. (ZMB 29310, n=1, some SEM material), west shore, north of Cape Sioloya, 02°50.386'S, 121°26.026'E, loc. 03-05, on rocks, coll. Y. Cai, K. & T. von Rintelen, 3 Jan.2005; 4 ex. (ZMB 29331), west shore, northeast shore, at Cape Noote, 02°39.751'S, 121°39.195'E, loc. 117-04, on rocks in deeper water, coll. K. & T. von Rintelen, 28 Jul.2004; 13 ex. (MZB Cru 1834, n=7; ZMB 29332, n=6), Cape Bakara, 02°40.771'S, 121°26.11'E, loc. 144-04, on rocks in deeper water, coll. K. & T. von Rintelen, 26 Jul.2004; 3 ex. (ZMB 29333), west shore, outlet bay, east of Cape Kombe, 02°48.08'S, 121°23.05'E, loc. 53-03, on rocks, coll. K. & T. von Rintelen, 21 Sep.2003; 4 ex. (ZMB 29334), west shore, west of Cape Timbalo, 02°42.631'S, 121°26.389'E, loc. 145-04, on rocks, coll. K. & T. von Rintelen, 26 Jul.2004.

**Description.** – Carapace length 2.4-3.8 mm (n=26). Rostrum (Fig. 47A; Table 17) long, reaching beyond end of scaphocerite, 1.0-1.6 times as long as carapace (n=20), armed dorsally with 13-22 teeth (including 3-4 teeth posterior to orbital margin), anterior less densely spaced, armed ventrally with 3-13 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.5-0.6 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.9-1.0 times as long as carapace (n=5), second segment 2.0-2.3 times length of third segment, third segment 0.3 times length of basal segment. Stylocerite reaching 0.9-1.0 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 47B) 4.7-5.6 times as long as wide (n=5).

Sixth abdominal somite 0.6-0.9 times length of carapace (n=26), 1.5-1.8 times as long as fifth somite (n=20), 0.9 times length of telson (n=7). Telson (Fig. 47E,H) 3.3-3.9 times as long as wide (n=5), distal margin rounded, without projection, with 3-4 pairs of spinules and 1 pair

of dorsolateral spinules; distal end with 4 pairs of spines, lateral pair distinctly longer than intermediate pairs, median pair not always shortest. Preanal carina (Fig. 47C) rounded, without a spine. Uropodal diaeresis (Fig. 47D) with 11-13 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereiopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipods only present on first pereiopod. Mouthparts as described by Cai et al. (2009).

Chela and carpus of first pereiopod distinctly stouter and broader than chela and carpus of second pereiopod (Fig. 47M-O); chela of first pereiopod 2.0-2.5 times as long as wide (n=20), 1.2-1.5 times length of carpus (n=26); tips of fingers rounded, without hooks; dactylus 1.0-1.5 times as long as palm (n=6); carpus 2.1-2.9 times as long as wide (n=20), 1.2-1.3 times length of merus (n=5). Chela of second

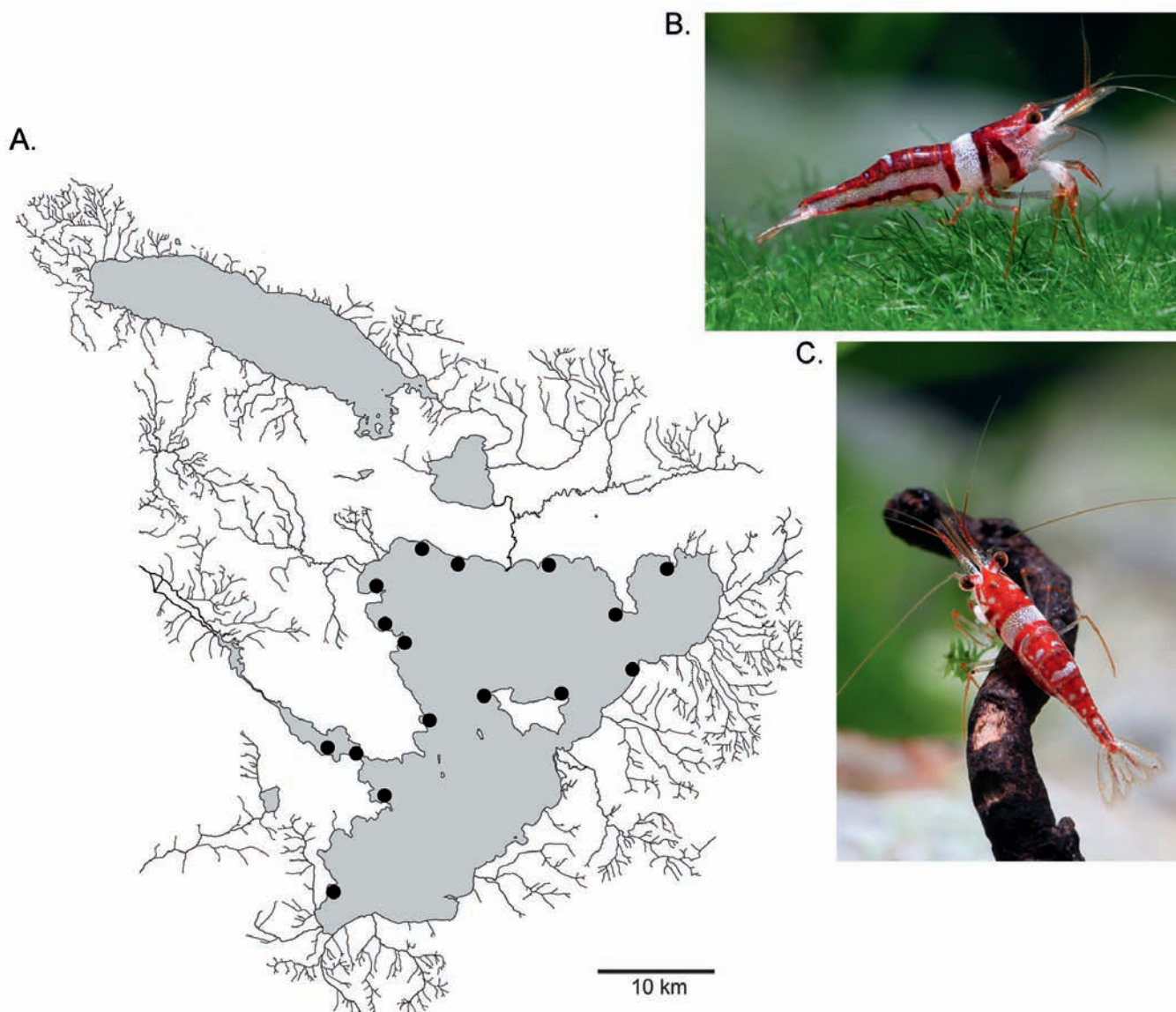


Fig. 46. *Caridina woltereckae* from the Malili lake system. A. Distribution. B.-C. Colour pattern of living animals (not to scale). Pictures courtesy of Chris Lukhaup.

Table 17. Summary of standard morphometric parameters for *Caridina woltereckae*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	2.4-3.8	2.8 $\pm$ 0.3	2.8	26
rl / cl	1.0-1.6	1.3 $\pm$ 0.2	1.3	20
n dorsal rostral teeth	13-22	18 $\pm$ 2	19	26
n ventral rostral teeth	3-13	8 $\pm$ 2	7	26
abds6 / cl	0.6-0.9	0.6 $\pm$ 0.1	0.6	26
abds6 / abds5	1.5-1.8	1.6 $\pm$ 0.1	1.6	20
abds6 / h tel	0.9	-	-	7
h tel / w tel	3.3-3.9	3.5 $\pm$ 0.3	3.4	5
n spines uropodal diaeresis	11-13	12 $\pm$ 1.0	13	5
h ch1 / w ch1	2.0-2.5	2.2 $\pm$ 0.1	2.3	20
h ch1 / h ca1	1.2-1.5	1.3 $\pm$ 0.1	1.3	26
h ca1 / w ca1	2.1-2.9	2.6 $\pm$ 0.2	2.6	20
h ch2 / w ch2	2.4-3.1	2.7 $\pm$ 0.2	2.7	20
h ch2 / h ca2	0.7-1.0	0.8 $\pm$ 0.0	0.8	25
h ca2 / w ca2	4.8-7.3	6.1 $\pm$ 0.7	6.1	20
n spines p3	1-2	2 $\pm$ 0	2	5
n spines p5	13-22	19 $\pm$ 4	20	5

pereiopod 2.4-3.1 times as long as wide (n=20), 0.7-1.0 times length of carpus (n=25); tips of fingers rounded, without hooks, dactylus 1.3-1.6 times as long as palm (n=6); carpus 4.8-7.3 times as long as wide (n=20), 1.4-1.5 times as long as merus (n=5).

Third pereiopod (Fig. 47F-G) slender, dactylus 2.8-4.0 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 1-2 accessory spines on flexor margin; propodus 12.5-17.0 times as long as wide, 4.8-6.5 times as long as dactylus; carpus 5.5-6.5 times as long as wide, 0.5-0.6 times as long as propodus, 0.5 times as long as merus; merus 9.2-9.9 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Fifth pereiopod slender (Fig. 47I-J), dactylus 3.4-4.5 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 13-22 accessory spines on flexor margin; propodus 16.0-22.0 times as long as wide, 4.4-5.8 times as long as dactylus; carpus 4.9-6.5 times as long as wide, 0.5-0.6 times as long as propodus, 0.6 times as long as merus; merus 9.1-10.0 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 47K) elongated triangular, 1.6-2.0 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 47L) 0.8-0.9 times length of appendix masculina (n=5).

Ovigerous females with 19-29 eggs (n=2 females); egg size 0.8-1.0 x 0.5-0.6 mm (n=48, eggs with eyes).

**Distribution.** – *C. woltereckae* is endemic to Lake Towuti, where it is widely distributed (Fig. 46A).

**Biology and ecology.** – *C. woltereckae* is a hard substrate dweller on smaller rocks mainly in shallow water, but also in deeper water regions (below 3 m) between larger rocks (boulders). When disturbed, it tries to escape side- or downwards rather than in other directions, but mainly stays attached to rocks. *C. woltereckae* is often found in syntopy with other rock dwellers in Lake Towuti, such as *C. profundicola*, *C. spinata*, *C. striata*, or *C. glaubrechtii*.

**Colour pattern.** – Carapace with three transversal dark brown (sometimes reddish) bands (Fig. 46B-C), first two usually joint at dorsal surface to form a n-shaped band in lateral view. Appendages are either transparent or slightly pigmented. Most parts of first and second pereiopods usually bright white, abdomen with a conspicuous white stripe expanding laterally along each side, dorsally densely covered with dark brown bands except for a white belt on the posterior of the carapace. Uropods with white-pigmented tips or unpigmented. Eggs usually dark brown. This colour pattern remains visible even if the shrimp is under stress, the intensity of the colour merely fades. When feeding, the white chelipeds were observed to be always clearly visible, whereas the rest of the (darker coloured) body was more or less camouflaged.

**Taxonomic remarks.** – The colour morph of living specimens closely resembles *C. spongicola*. Therefore, both species can easily be confused in the field, although *C. woltereckae* is a typical rock dweller and has a much wider distribution (vs. sponge dweller and restricted to the outlet bay of Lake Towuti). It is generally also larger (carapace length 2.4-3.8, median 2.8 vs. in 1.8-2.8, median 2.4 in *C. spongicola*) and has a longer rostrum (reaching beyond end of scaphocerite



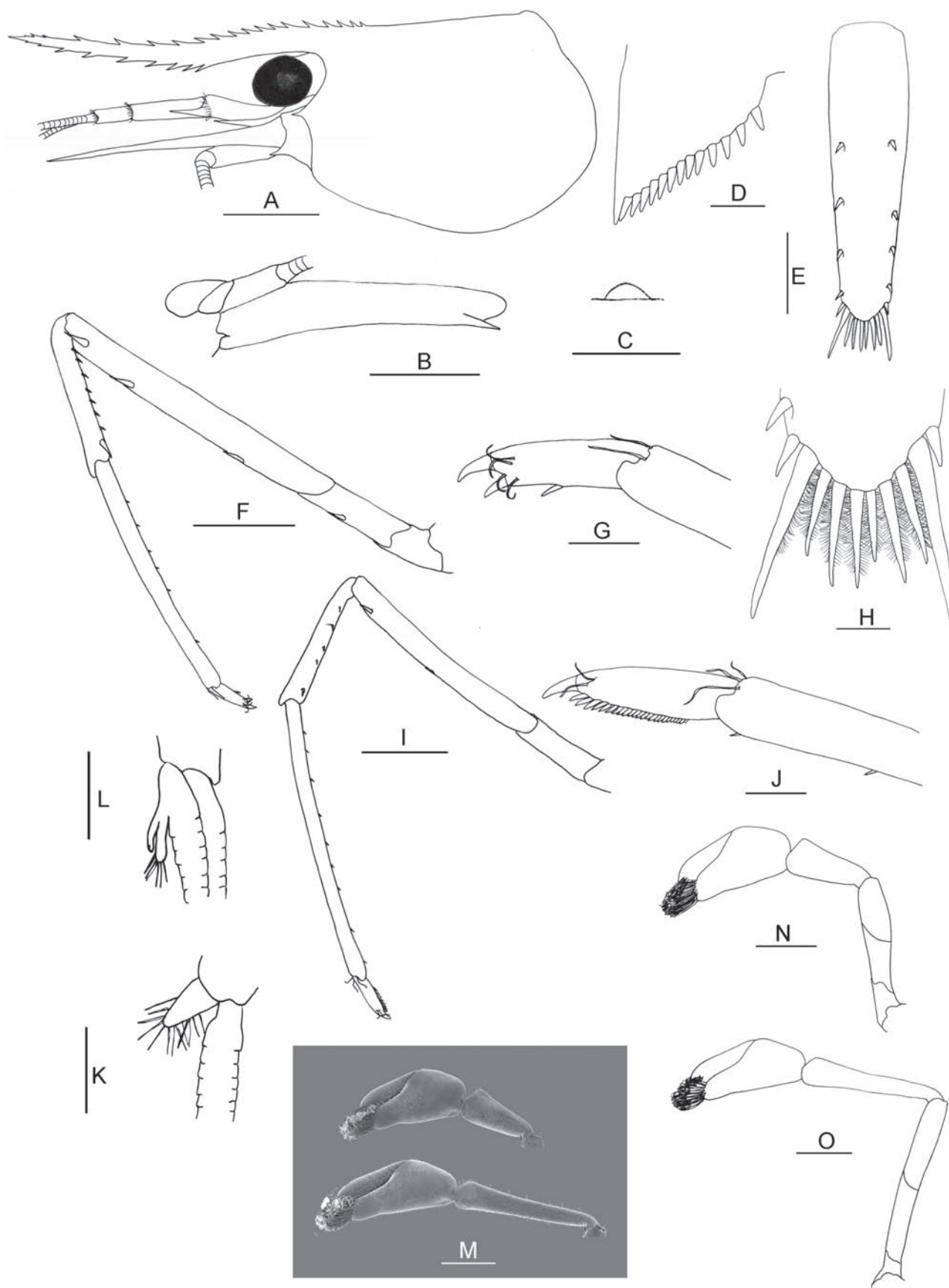


Fig. 47. *Caridina woltereckae* from the Malili lake system. A. Cephalothorax and cephalic appendages, female (ZMB 29052); B. Scaphocerite, female (ZMB 29037); C. Preanal carina; D. Uropodal diaeresis, female (ZMB 29310); E. Telson, F. Third pereiopod, female (ZMB 29147); G. Dactylus of third pereiopod; H. Distal end of telson, female (ZMB 29310); I. Fifth pereiopod, female (ZMB 29147); J. Dactylus of fifth pereiopod; K. Endopod of male first pleopod (ZMB 29037); L. Appendix masculina of male second pleopod; M. SEM image of chela and carpus of first and second pereiopods, female (ZMB 29052); N. First pereiopod, female (ZMB 29052); O. P. Second pereiopod. Scale bars: A-B = 1.0 mm; C, E-F, I, K-O = 0.5 mm; D, G-H, J = 0.1 mm.

vs. reaching to or slightly beyond third segment of antennular peduncle in *C. spongicola*). As alcohol bleached material, *C. woltereckae* is almost identical with *C. striata* and *C. glaubrechti*, although the colour pattern in living specimens always allows an unambiguous separation. It slightly differs from both by a lower number of spines on the dactylus of the fifth pereopod (13-22, median 20 vs. 14-35, median 28 in *C. glaubrechti* and 24-35, median 33 in *C. striata*). Also the dimorphic character of the rostrum in *C. striata* could not be observed in *C. woltereckae*.

In the molecular phylogeny (Figs. 63-64), *C. woltereckae* forms a single clade with the other rock dwellers *C. striata* and *C. glaubrechti*, and the sponge dweller *C. spongicola*, but their relationship is not resolved within this clade (compare von Rintelen et al., 2007b; for further details see taxonomic remarks on *C. striata*).

### SPECIES FROM LAKE POSO (INDONESIA, CENTRAL SULAWESI)

#### *Caridina acutirostris* Schenkel, 1902

(Figs. 48–50; Table 18)

*Caridina acutirostris* Schenkel, 1902: 496, pl. 8, Figs. 3a-c, 4b (type locality: area south of Lake Poso, approx. 600 m above sealevel).

*Caridina acutirostris* – Roux, 1904: 551; Bouvier, 1905: 73, 1925: 166, Figs. 353-355; Chace, 1997: 6; Cai & Wowor, 2007: 314; von Rintelen et al., 2007a: 1033, fig. 2; Tables 1-2, 2008: 2244, Table 1.

**Material examined.** – Holotype: female (cl 5.2mm) (NHMB 3a), area south of Lake Poso, approx. 600 m above sealevel, coll. Sarasin, 1907.

Lake Poso catchment: 14 ex. (MZB Cru 1843, n=7; ZMB 29439, n=7), Tonusu, approx. 3 km south of Tonusu towards Siuri, 01°48.95'S, 120°31.18'E, loc. 185-05, on macrophytes, coll. K. von Rintelen, 6 Oct.2005; 11 ex. (MZB Cru 1844, n=5; ZMB 29440, n=6 and some juveniles, some SEM material), stream south of Pendolo, 02°8.702'S, 120°43.854'E, loc. 196-05, on roots, coll. K. von Rintelen, 8 Oct.2005.

**Description.** – Carapace length 3.1-5.8 mm (n=11). Rostrum (Fig. 49A-C; Table 18) short, usually shorter than scaphocerite, reaching to or near distal end of second segment of antennular peduncle, in large females sometimes reaching near end of scaphocerite, 0.3-0.7 times as long as carapace (n=11), armed dorsally with 10-13 teeth (including 3-4 teeth posterior to orbital margin), about anterior third to half unarmed, without subapical teeth, armed ventrally with 4-9 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.6-0.7 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.7-1.1 times as long as carapace (n=5), second segment 1.4-1.8 times length of third segment, third segment 0.3-0.4 times length of basal segment. Stylocerite reaching 0.9-1.0 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 49D) 3.0-3.6 times as long as wide (n=5).

Sixth abdominal somite 0.6 times length of carapace (n=9), 1.7-2.0 times as long as fifth somite (n=5), 0.9-1.0 times length of telson (n=5). Telson (Fig. 49G,J) 3.0-3.3 times as long as wide (n=5), distal margin rounded, without projection, with 4-5 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 4-5 pairs of spines. Preanal carina (Fig. 49E) with a spine. Uropodal diaeresis (Fig. 49F) with 11-17 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipods present on first two pereopod, reduced or totally absent from third pereopod. Incisor process of mandible (Fig. 50A) ending in a row of 3-5 small teeth, molar process truncated. Lower lacinia of maxillula (Fig. 50B) broadly rounded, upper lacinia elongate, with numerous distinct teeth and setae on inner margin, palp slender. Upper endites of maxilla (Fig. 50C) subdivided, palp short, scaphognathite tapering posteriorly with numerous long, curved setae at posterior end. Distal end of palp of first maxilliped (Fig. 50F) triangular, ending with a short finger-like projection; flagellum of the exopod elongated, endopod high, not exceeding the flagellum of

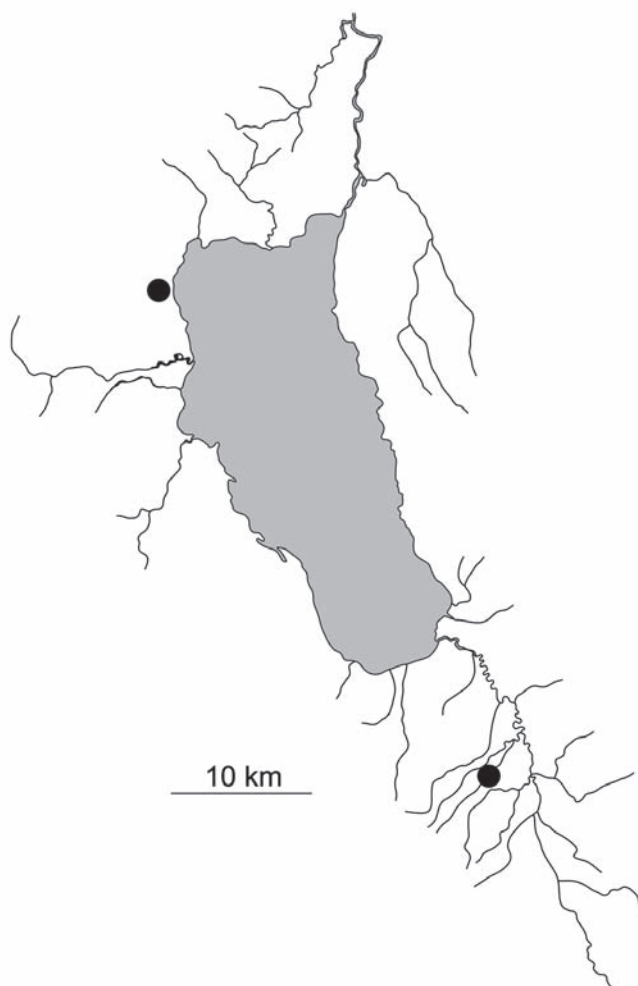


Fig. 48. Distribution of *Caridina acutirostris* in the Poso catchment.

Table 18. Summary of standard morphometric parameters for *Caridina acutirostris*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	3.1-5.8	4.3 $\pm$ 0.7	4.1	11
rl / cl	0.3-0.7	0.5 $\pm$ 0.1	0.5	11
n dorsal rostral teeth	10-13	11 $\pm$ 1	11	11
n ventral rostral teeth	4-9	5 $\pm$ 2	4	11
abds6 / cl	0.6	-	-	9
abds6 / abds5	1.7-2.0	1.8 $\pm$ 0.1	1.8	5
abds6 / h tel	0.9-1.0	1.0 $\pm$ 0.0	1.0	5
h tel / w tel	3.0-3.3	3.1 $\pm$ 0.1	3.1	5
n spines uropodal diaeresis	11-17	14 $\pm$ 2	13	5
h ch1 / w ch1	2.0-2.6	2.3 $\pm$ 0.2	2.2	8
h ch1 / h ca1	1.2-1.3	1.3 $\pm$ 0.0	1.3	8
h ca1 / w ca1	2.0-2.7	2.2 $\pm$ 0.3	2.1	8
h ch2 / w ch2	2.9-3.4	3.2 $\pm$ 0.2	3.2	8
h ch2 / h ca2	0.8-0.9	0.8 $\pm$ 0.0	0.8	8
h ca2 / w ca2	4.5-5.9	5.1 $\pm$ 0.5	4.9	8
n spines p3	4-9	6 $\pm$ 2	6	5
n spines p5	45-66	55 $\pm$ 7.6	55	5

exopod in length. Second maxilliped (Fig. 50D) typical. Third maxilliped (Fig. 50E) with ultimate segment slightly shorter than penultimate segment.

Chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig. 49O-Q); chela of first pereopod 2.0-2.6 times as long as wide (n=8), 1.2-1.3 times length of carpus (n=8); tips of fingers rounded, without hooks; dactylus 0.7-1.4 times as long as palm (n=5); carpus 2.0-2.7 times as long as wide (n=8), 1.1-1.2 times length of merus (n=5). Chela of second pereopod 2.9-3.4 times as long as wide (n=8), 0.8-0.9 times length of carpus (n=8); tips of fingers rounded, without hooks, dactylus 1.0-1.4 times as long as palm (n=5); carpus 4.5-5.9 times as long as wide (n=8), 1.4-1.6 times as long as merus (n=5).

Dactylus of third pereopod (Fig. 49H,K) 3.2-3.9 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 4-9 accessory spines on flexor margin; propodus 8.6-11.1 times as long as wide, 3.3-3.7 times as long as dactylus; carpus 4.6-5.7 times as long as wide, 0.6-0.7 times as long as propodus, 0.5 times as long as merus; merus 7.1-9.2 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface. Dactylus of fifth pereopod (Fig. 49I,L) 4.0-5.6 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 45-66 accessory spines on flexor margin; propodus 10.0-12.5 times as long as wide, 2.9-3.2 times as long as dactylus; carpus 4.1-5.5 times as long as wide, 0.5 times as long as propodus, 0.6 times as long as merus; merus 6.7-7.9 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 49M) elongated triangular, 2.1-2.4 times as long as proximally wide (n=4),

without appendix interna. Appendix interna of male second pleopod (Fig. 49N) 0.7-0.8 times length of appendix masculina (n=4).

Ovigerous females with 23-54 eggs (n=2 females); egg size 1.1-1.3 x 0.7-0.8 mm (n=20, eggs with and without eyes).

**Distribution.** – *C. acutirostris* is endemic to the Poso river catchment occurring in streams around the lake (Fig. 48). So far only known from two distant localities, the southern one is the type locality “Salukuwa and other small streams, drainage of Kodina River, south of Lake Poso”, where Fritz and Paul Sarasin collected the specimens of *C. acutirostris* (Sarasin & Sarasin, 1905: 238) later described by Schenkel (1902).

In the molecular phylogeny (Figs. 63,65), two specimens referred to as *C. cf. acutirostris* from the Tomori region cluster with specimens of *C. acutirostris* (compare von Rintelen et al., 2007a). These have not been included here due to differences in morphology and their geographic origin. Their taxonomic status awaits further investigation.

**Biology and ecology.** – *C. acutirostris* is an exclusively riverine species that was collected from vegetation (green parts and roots). It was never found in sympatry with the other riverine species endemic to the Poso system (*C. schenkeli*).

**Colour pattern.** – Without any species specific pattern. Body colouration transparently yellowish or brownish, typical for riverine species from all over Sulawesi. Large (often ovigerous) females usually appear darker than smaller specimens.

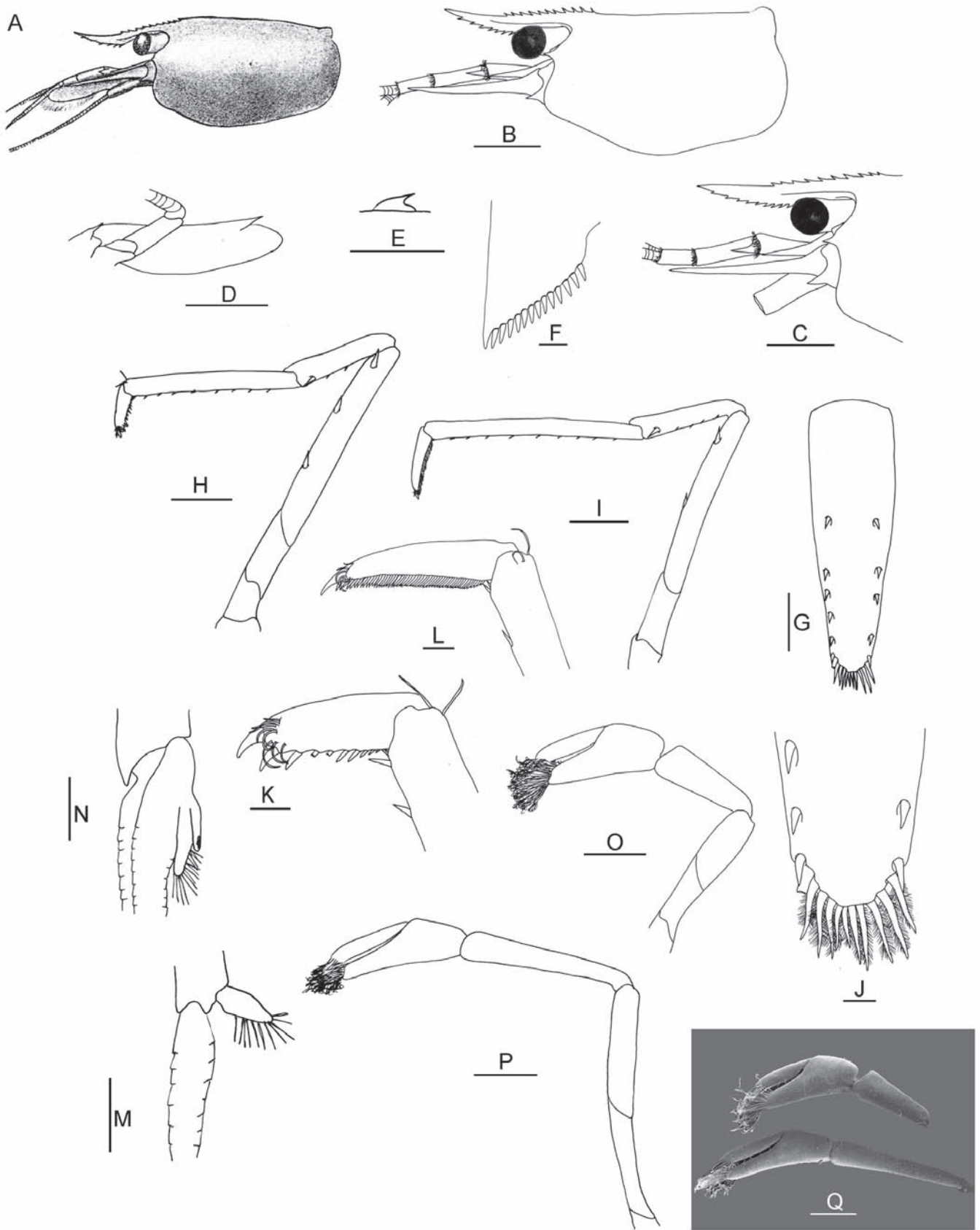


Fig. 49. *Caridina acutirostris* from the Lake Poso catchment. A. Schenkel's drawing of cephalothorax and cephalic appendages (modified from 1902); B. Cephalothorax and cephalic appendages, male (ZMB 29440); C. Cephalothorax and cephalic appendages, another male (ZMB 29440); D. Scaphocerite, female (ZMB 29440); E. Preanal carina, F. Uropodal diaeresis, male (ZMB 29440); G. Telson; H. Third pereiopod; I. Fifth pereiopod; J. Distal end of telson; K. Dactylus of third pereiopod; L. Dactylus of fifth pereiopod; M. Endopod of male first pleopod; N. Appendix masculina of male second pleopod; O. First pereiopod; P. Second pereiopod; Q. SEM image of chela and carpus of first and second pereiopods. Scale bars: B-D = 1.0 mm; E, G-I, M-Q = 0.5 mm; F, J-L = 0.1 mm; A = no scale available.

**Taxonomic remarks.** – *C. acutirostris* differs from all Poso species by the short rostrum (usually not reaching end of scaphocerite vs. longer in all other species) and the ratio of rostrum to carapace length (0.3-0.7, median 0.5 vs. over 0.7 in the other species). With regard to the rostrum and body size, *C. acutirostris* mainly resembles *C. schenkeli* (carapace length in mm 3.1-5.8, median 4.1 and 3.6-5.1, median 4.2 in *C. schenkeli*), but differs by the length of the rostrum (shorter in *C. acutirostris*), and a lower number of ventral rostral teeth (4-9, median 4 vs. 9-13, median 11 in *C.*

*schenkeli*). Further, *C. acutirostris* can resemble specimens of *C. mahalona* (Malili lakes) with a short rostrum, although the scaphocerite usually is stouter (3.0-3.6 times as long as wide vs. 3.5-4.1 times as long as wide in *C. mahalona*). Further, the carpus of the first and second pereopod is stouter (2.0-2.7 and 4.5-5.9 times as long as wide vs. 2.5-3.3 and 5.6-7.0 times as long as wide in *C. mahalona*). The general range of parameters (for example the number of rostral teeth) is usually higher in *C. mahalona* than in *C. acutirostris* (Tables 10,19).

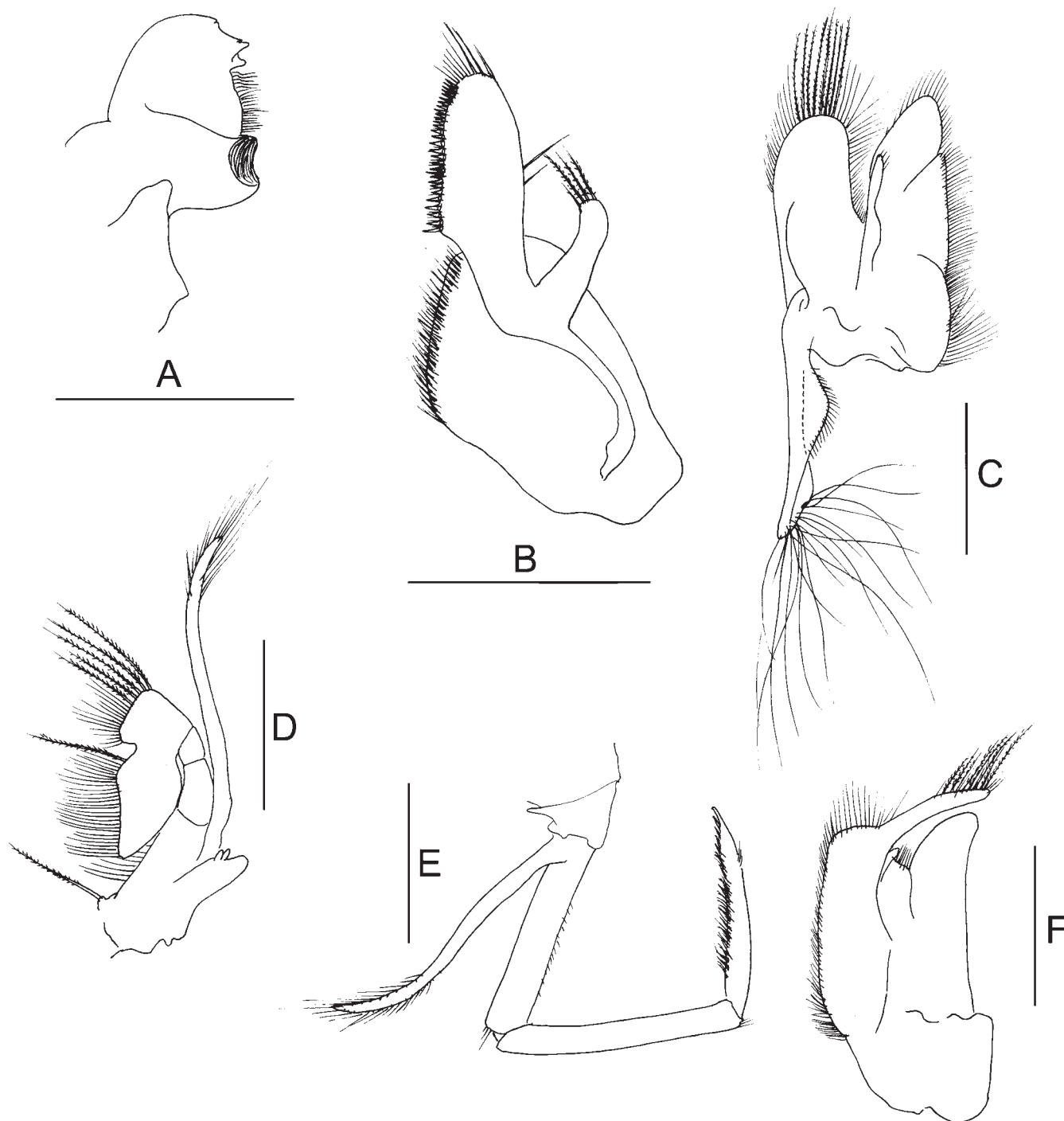


Fig. 50. *Caridina acutirostris* from the Lake Poso catchment. A. Mandible (ZMB 29440); B. Maxillula; C. Maxilla; D. second maxilliped; E. third maxilliped; F. first maxilliped. Scale bars: A-F = 1mm.

In the molecular phylogeny (Figs. 63, 65) *C. acutirostris* is genetically distinct from all other Poso species, however appears within the Poso clade (for a detailed discussion see von Rintelen et al., 2007a).

***Caridina caerulea*, new species**

(Figs. 51–53; Tables 19–20)

*Caridina ensifera* Schenkel, 1902 pro parte: 490, pl. 8, Figs. 1a-e, 4d (type locality: Lake Poso).

*Caridina ensifera* – Cai & Wowor, 2007 pro parte: 311, Figs. 1-2.

*Caridina ensifera* “blue” – von Rintelen et al., 2007a: 1034, Figs. 1-2, Tables 1-2.

**Material examined.** – Holotype – male (cl 4.4 mm)(MZB Cru 2123), Lake Poso, west shore, Cape Bancea, 01°59.023'S, 120°35.108'E, loc. 59-04, on rocks in shallow water, coll. M. Glaubrecht & T. von Rintelen, 29 Mar.2004.

Paratypes (Lake Poso) – 1 ex. (ZMB 29207), east shore, 01°59.867'S, 120°41.238'E, loc. 160-04, on mixed substrate, coll. K. & T. von Rintelen, 16 Aug.2004; 17 ex. (MZB Cru 1718, n=9; ZMB 29251, n=8, some SEM material), south shore, Pendolo, beach at Hotel Mulia, 02°3.876'S, 120°41.587'E, loc. 50-04, on wood, coll. M. Glaubrecht & T. von Rintelen, 27 Mar.2004; 16 ex. (MZB Cru 1719, n=7; ZMB 29260, n=9, some SEM material), west shore, Cape Bancea, 01°59.023'S, 120°35.108'E, loc. 59-04, on rocks in shallow water, coll. M. Glaubrecht & T. von Rintelen, 29 Mar.2004; 1 ex. (ZMB 29290, n=1 and some juveniles, some SEM material), south shore, Pendolo beach at Hotel Mulia, 02°3.928'S, 120°41.536'E, loc. 157-04, on wood, coll. K. & T. von Rintelen, 15 Aug.2004; 8 ex. (ZMB 29292a, n=2; ZMB 29292b, n=6), east shore, south of Cape Sinampada, 01°56.25'S, 120°40.443'E, loc. 159-04, (a) on rocks in deeper water (approx. 13 m), (b) on macrophytes, coll. M. Glaubrecht & T. von Rintelen, 29 Mar.2004; 5 ex. (ZMB 29306), east shore, Tando Bone, 01°50.0'S, 120°38.004'E, loc. 157-05, on wood, coll. K. von Rintelen, 3 Oct.2005; 13 ex. (MZB Cru 1720, n=6; ZMB 29325, n=7), west shore, Siuri, 01°48.259'S, 120°31.667'E, loc. 186-05, on mixed substrate, coll. K. von Rintelen, 6 Oct.2005; 4 ex. (ZMB 29382), north shore, 01°47.162'S, 120°33.144'E, loc.

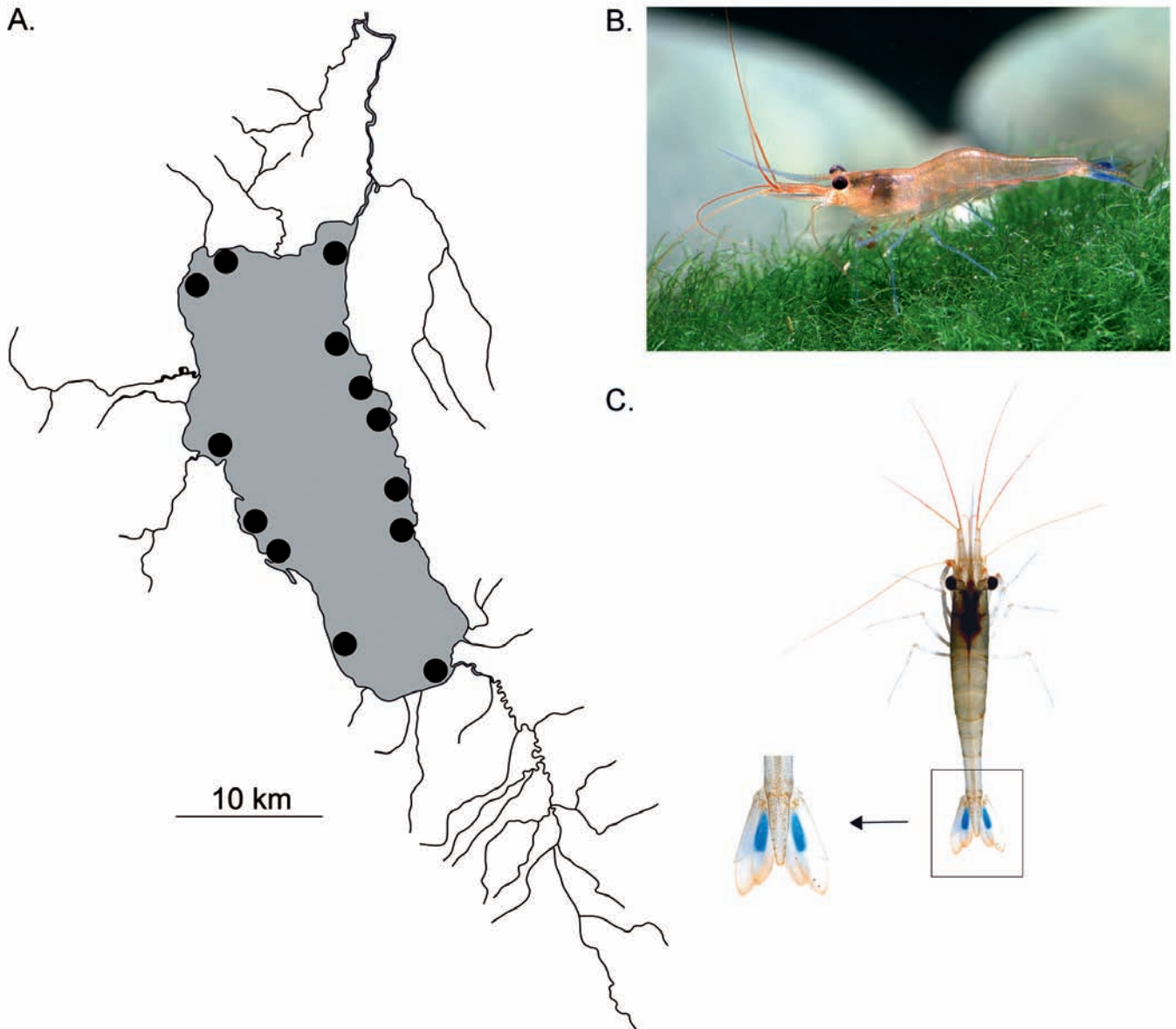


Fig. 51. *Caridina caerulea* from Lake Poso. A. Distribution. B-C. Colour pattern of living animals (not to scale). Picture B. courtesy of Chris Lukhaup.

Table 19. Summary of standard morphometric parameters for *Caridina caerulea*.

cl (mm)	3.0-4.5	3.7 ± 0.4	3.7	40
rl / cl	1.9-2.6	2.2 ± 0.2	2.2	40
n dorsal rostral teeth	11-20	15 ± 2	16	40
n ventral rostral teeth	26-48	34 ± 5	34	40
abds6 / cl	0.4-0.8	0.7 ± 0.1	0.7	40
abds6 / abds5	1.0-2.5	2.0 ± 0.2	2.0	40
abds6 / h tel	0.9-1.0	0.9 ± 0.0	0.9	5
h tel / w tel	3.5-4.1	3.8 ± 0.3	3.9	5
n spines uropodal diaeresis	11-14	12 ± 1.1	12	5
h ch1 / w ch1	1.9-2.7	2.2 ± 0.2	2.2	40
h ch1 / h ca1	0.9-1.5	1.3 ± 0.1	1.3	40
h ca1 / w ca1	1.9-5.1	2.4 ± 0.5	2.4	40
h ch2 / w ch2	2.1-3.2	2.7 ± 0.2	2.7	40
h ch2 / h ca2	0.6-1.4	0.8 ± 0.1	0.8	40
h ca2 / w ca2	2.2-6.0	5.0 ± 0.6	5.0	40
n spines p3	4-5	5 ± 1	5	5
n spines p5	27-49	36 ± 9	35	5

Table 20. Comparison of the rostrum denticulation in *Caridina ensifera* based on the original description (modified from Schenkel, 1902: tables on pages 493 and 495) and this study.

parameter	range	mean ± SD	median	n
Rostrum original description (Schenkel, 1902)				
n dorsal rostral teeth	9-20	14 ± 3	13	36
n ventral rostral teeth	8-26	17 ± 5	17	36
Rostrum <i>C. ensifera</i> this study				
n dorsal rostral teeth	9-15	12 ± 2	12	40
n ventral rostral teeth	16-29	22 ± 3	23	40
Rostrum <i>C. caerulea</i> , new species				
n dorsal rostral teeth	11-20	15 ± 2	16	40
n ventral rostral teeth	26-48	34 ± 5	34	40

187-05, on rocks, coll. K. von Rintelen, 6 Oct.2005; 6 ex. (ZMB 29385), west shore, 02°2.734'S, 120°37.368'E, loc. 178-05, on wood, coll. K. von Rintelen, 6 Oct.2005; 4 ex. (ZMB 29393), east shore, at road Tentena-Peura, 01°47.33'S, 120°38.079'E, loc. 160-05, on wood, coll. K. von Rintelen, 3 Oct.2005; 8 ex. (MZB Cru 1721, n=4; ZMB 29394, n=4), west shore, 01°58.21'S, 120°34.316'E, loc. 181-05, on wood, coll. K. von Rintelen, 6 Oct.2005; 13 ex. (MZB Cru 1722, n=6; ZMB 29395, n=7, some SEM material), east shore, bay at Cape Nceppo, 01°52.39'S, 120°38.974'E, loc. 156-05, on mixed substrate, coll. K. von Rintelen, 3 Oct.2005; 7 ex. (MZB Cru 1723, n=3; ZMB 29400, n=4), east shore, shallow bay at Cape Songuo, 01°53.748'S, 120°39.939'E, loc. 155-05, on mixed substrate, coll. R. Lamers & K. von Rintelen, 3 Oct.2005; 1 ex. (ZMB 29405), west shore, Taipa, 01°55.289'S, 120°32.77'E, loc. 182-05, on wood, coll. K. von Rintelen, 6 Oct.2005.

**Description.** – Carapace length 3.0-4.5 mm (n=40). Rostrum (Fig. 52A; Tables 19-20) very long and slender, reaching far beyond end of scaphocerite, 1.9-2.6 times as long as carapace (n=40), armed dorsally with 11-20 teeth (including

2-4 teeth posterior to orbital margin), approx. anterior 2/3 unarmed, without subapical teeth, armed ventrally with 26-48 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.5-0.6 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.9-1.1 times as long as carapace (n=5), second segment 1.8-2.0 times length of third segment, third segment 0.3 times length of basal segment. Stylocerite reaching 0.8-1.0 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 52D) 3.6-4.8 times as long as wide (n=5).

Sixth abdominal somite 0.4-0.8 times length of carapace (n=40), 1.0-2.5 times as long as fifth somite (n=40), 0.9-1.0 times length of telson (n=5). Telson (Fig. 52C,J) 3.5-4.1 times as long as wide (n=5), distal margin rounded, without projection, with 4-5 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 2-3 pairs of spines, lateral pair distinctly longer than intermediate pairs. Preanal carina (Fig.

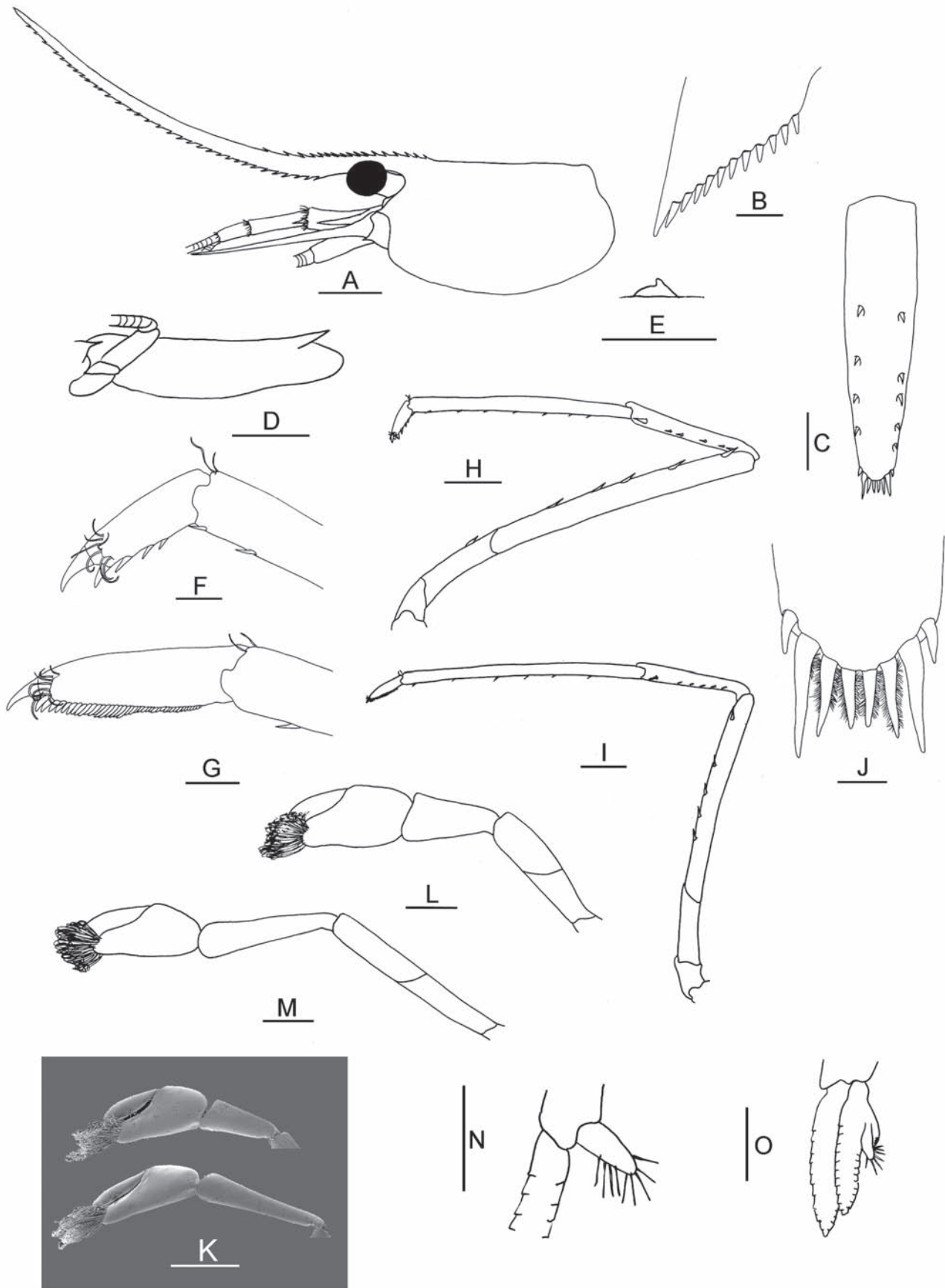


Fig. 52. *Caridina caerulea* from Lake Poso. A. Cephalothorax and cephalic appendages, male (ZMB 29251); B. Uropodal diaeresis; C. Telson, female (ZMB 29251); D. Scaphocerite, female (ZMB 29393); E. Preanal carina, F. Dactylus of third pereiopod, male (ZMB 29395); G. Dactylus of fifth pereiopod; H. Third pereiopod; I. Fifth pereiopod; J. Distal end of telson, female (ZMB 29251); K. SEM image of chela and carpus of first and second pereiopods, female (ZMB 29251); L. First pereiopod, male (ZMB 29260); M. Second pereiopod; N. Endopod of male first pleopod (ZMB 29393); O. Appendix masculina of male second pleopod. Scale bars: A, D = 1.0 mm; C, E, H-I, K-O = 0.5 mm; B, F-G, J = 0.1 mm.



52E) with a spine. Uropodal diaeresis (Fig. 52B) with 11-14 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereiopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipods present on first two pereiopods. Incisor process of mandible (Fig. 53A) ending in a row of 3-4 small teeth, molar process truncated. Lower lacinia of maxillula (Fig. 53B) broadly rounded, upper lacinia elongate, with numerous distinct teeth and setae on inner margin, palp slender. Upper endites of maxilla (Fig. 53C) subdivided, palp short, scaphognathite tapering posteriorly

with numerous long, curved setae at posterior end. Distal end of palp of first maxilliped (Fig. 53F) triangular, ending with a short finger-like projection; flagellum of the exopod short and stout, endopod high, almost reaching end of the flagellum of exopod. Second maxilliped (Fig. 53E) typical. Third maxilliped (Fig. 53D) with ultimate segment as long as penultimate segment.

Chela and carpus of first pereiopod distinctly stouter and broader than chela and carpus of second pereiopod (Fig. 52K-M); chela of first pereiopod 1.9-2.7 times as long as wide (n=40), 0.9-1.5 times length of carpus (n=40); tips of fingers rounded, without hooks; dactylus 1.1-1.4 times as long as palm (n=5); carpus 1.9-5.1 times as long as wide

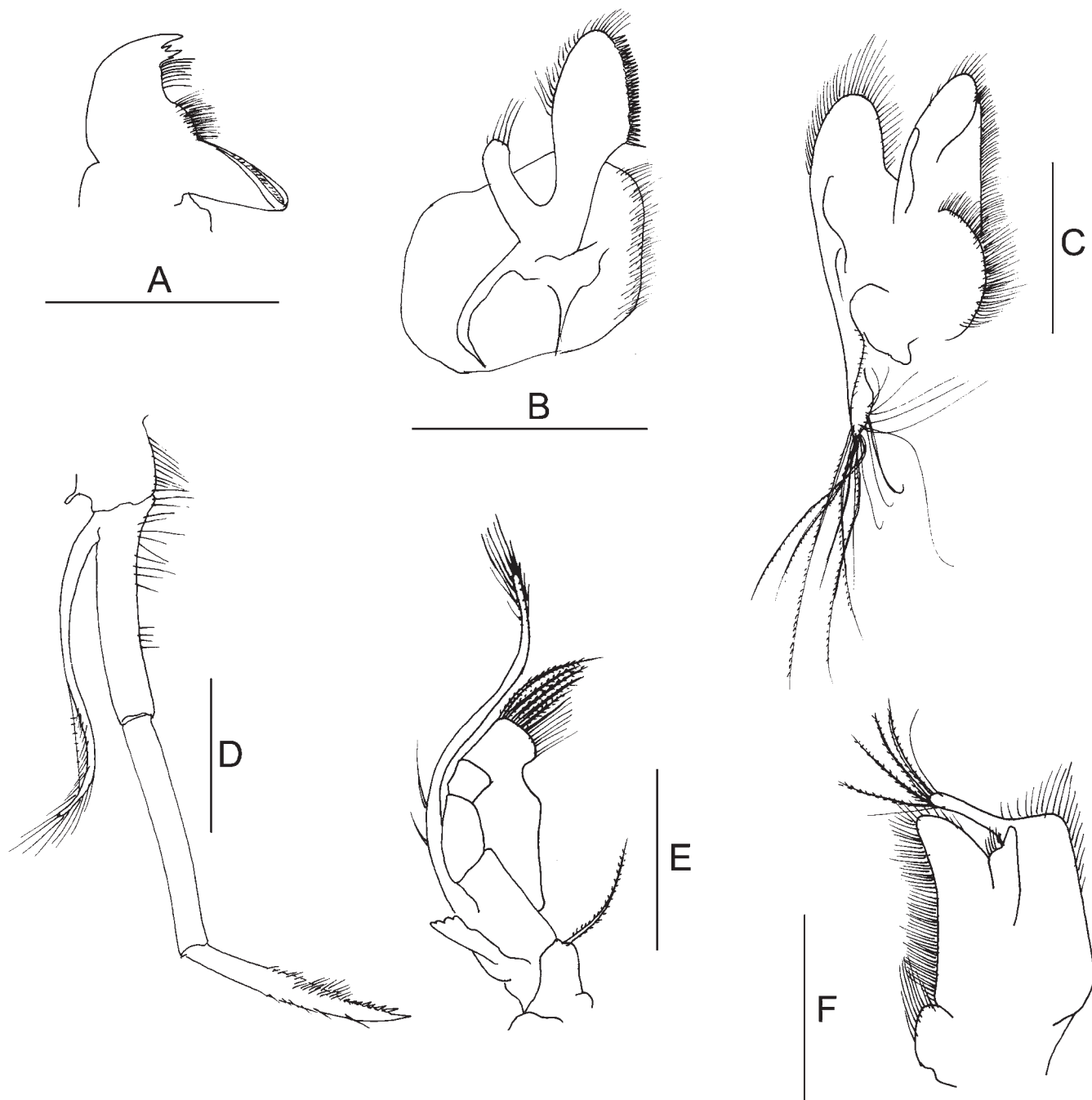


Fig. 53. *Caridina caerulea* from the Lake Poso catchment. A. Mandible (ZMB 29260); B. Maxillula; C. Maxilla; D. third maxilliped; E. second maxilliped; F. first maxilliped. Scale bars: A-F = 1mm.

(n=40), 1.1-1.3 times length of merus (n=5). Chela of second pereopod 2.1-3.2 times as long as wide (n=40), 0.6-1.4 times length of carpus (n=40); tips of fingers rounded, without hooks, dactylus 1.3-1.6 times as long as palm (n=5); carpus 2.2-6.0 times as long as wide (n=40), 1.3-1.6 times as long as merus (n=5).

Third pereopod (Fig. 52F,H) slender, dactylus 3.0-3.8 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 4-5 accessory spines on flexor margin; propodus 12.9-16.3 times as long as wide, 5.0-6.0 times as long as dactylus; carpus 5.9-8.0 times as long as wide, 0.5-0.6 times as long as propodus, 0.5 times as long as merus; merus 9.4-11.8 times as long as wide, bearing 3-5 strong, movable spines on posterior margin of outer surface.

Fifth pereopod slender (Fig. 52G,I), dactylus 3.6-5.0 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 27-49 accessory spines on flexor margin; propodus 15.8-22.3 times as long as wide, 4.3-6.0 times as long as dactylus; carpus 6.2-7.2 times as long as wide, 0.5-0.6 times as long as propodus, 0.5-0.6 times as long as merus; merus 8.5-11.3 times as long as wide, bearing 3-5 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 52N) elongated triangular, 2.1-2.8 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 52O) 0.8-0.9 times length of appendix masculina (n=5).

Ovigerous females with 16-32 eggs (n=2 females); egg size 0.9-1.1 x 0.6-0.7 mm (n=25, eggs with and without eyes).

**Distribution.** – Endemic to Lake Poso (excluding rivers) and widely distributed within the lake (Fig. 51A), although not as abundant as *C. ensifera*.

**Biology and ecology.** – *C. caerulea* was mainly found on hard substrate (wood, rocks, but also sporadically on soft substrate, for example macrophytes; compare von Rintelen et al., 2007a).

**Colour pattern.** – Body transparently yellowish or reddish, antennules reddish; legs and rostrum bluish (Fig. 51B). The most conspicuous pattern is visible on the tailfan, each endopod bearing an elongated blue patch (upside down V-shape) on the distal part (Fig. 51C).

**Etymology.** – The name *Caridina caerulea* refers to the conspicuous colour pattern of this new species (the Latin word *caeruleus* means blue). *C. caerulea* is the only ancient lake shrimp exhibiting a partly blue body colouration.

**Taxonomic remarks.** – Of all Lake Poso species, *C. caerulea* closely resembles *C. ensifera*. Therefore, both taxa can easily be confused as alcohol bleached material, although in living specimens the colour pattern (“blue” vs.

“red” in *C. ensifera*; compare von Rintelen et al. 2007a) always allows an unambiguous separation, even in juveniles. Additionally, they show different substrate preferences and behaviour (rather stationary on hard substrate, i.e. rock and wood, vs. often pelagic on various kinds of substrate in *C. ensifera*). Although *C. caerulea* is almost identical with *C. ensifera* (excluding the always distinct colour pattern), it can be distinguished by not only a generally higher number of rostral teeth (Table 20), but also by a higher number of spines on the uropodal diaeresis (11-14, median 12 vs. 9-11, median 10 in *C. ensifera*) and by a lower number of spines on the third and fifth pereopod (4-5, median 5 and 27-49, median 35 vs. 6-9, median 6 and 51-57, median 52 in *C. ensifera*).

The morphological results are well supported by molecular data (Figs. 63,65), placing *C. caerulea* and *C. ensifera* in two separate clades that are not even sister groups (for a detailed discussion see von Rintelen et al., 2007a).

***Caridina ensifera* Schenkel, 1902**  
(Figs. 54–55; Tables 20–21)

*Caridina ensifera* Schenkel, 1902 pro parte: 490, pl. 8, Figs. 1a-e, 4d (type locality: Lake Poso).

*Caridina ensifera* – Roux, 1904: 552; Bouvier, 1904: 131, 1905: 73, 1912: 918, 1913a: 463; 1913b: 182, 1925: 163, Figs. 344-352; Chace, 1997: 9; Fernandez-Leborans & von Rintelen, 2007; Cai & Wowor, 2007 pro parte: 311, Figs. 1-2; von Rintelen et al., 2007a: 1033, Figs. 1-2; Tables 1-2, 2008: 2244, Table 1.

**Material examined.** – Lectotype: male (cl 3.9 mm) (NHMB 1a), Indonesia, Sulawesi, Lake Poso, coll. Sarasin, no date indicated.

Paralectotypes – 5 males (cl 3.1-3.5 mm), 10 females (cl 3.0-5.3 mm) (NHMB 1a), same data as lectotype.

Others (Lake Poso): 16 ex. (MZB Cru 1709, n=8; ZMB 29248, n=8, some SEM material), south shore, Pendolo beach at Hotel Mulia, 02°3.928'S, 120°41.536'E, loc. 157-04, on wood, coll. K. & T. von Rintelen, 15 Aug.2004; 10 ex. (MZB Cru 1710, n=5; ZMB 29253, n=5, some SEM material), east shore, Cape Watulunto, 02°0.825'S, 120°42.007'E, loc. 63-04, on mixed substrate, coll. M. Glaubrecht & T. von Rintelen, 30 Mar.2004; 5 ex. (ZMB 29291), east shore, south of Cape Panti, 02°55.277'S, 120°40.289'E, loc. 158-04, on macrophytes, coll. K. & T. von Rintelen, 16 Aug.2004; 4 ex. (ZMB 29381), north shore, 01°47.162'S, 120°33.144'E, loc. 187-05, on rocks, coll. K. von Rintelen, 6 Oct.2005; 9 ex. (MZB Cru 1711, n=4; ZMB 29384, n=5), west shore, Siuri, 01°48.259'S, 120°31.667'E, loc. 186-05, pelagic, coll. K. von Rintelen, 6 Oct.2005; 20 ex. (MZB Cru 1712, n=10; ZMB 29389, n=10, some SEM material), east shore, bay at Cape Nceppo, 01°52.39'S, 120°38.974'E, loc. 156-05, on mixed substrate, coll. K. von Rintelen, 3 Oct.2005; 14 ex. (MZB Cru 1713, n=7; ZMB 29392, n=7), west shore, 02°2.734'S, 120°37.368'E, loc. 178-05, on mixed substrate, coll. K. von Rintelen, 6 Oct.2005; 21 ex. (MZB Cru 1714, n=10; ZMB 29396, n=11), west shore, 01°58.21'S, 120°34.316'E, loc. 181-05, on mixed substrate, coll. K. von Rintelen, 6 Oct.2005; 7 ex. (MZB Cru 1715, n=3; ZMB 29397, n=4), east shore, at road Tentena-Peura, 01°47.33'S, 120°38.079'E, loc. 160-05, on rocks, coll. K. von Rintelen, 3 Oct.2005; 8 ex. (MZB Cru 1716, n=4; ZMB 29399, n=4 and some juveniles), east shore, shallow bay, 01°49.702'S, 120°38.161'E, loc. 159-05, on macrophytes, coll. K. von Rintelen,

3 Oct.2005; 17 ex. (MZB Cru 1717, n=8; ZMB 29404, n=9, some SEM material), west shore, 01°52.205'S, 120°32.281'E, loc. 184-05, pelagic, coll. R. Lamers & K. von Rintelen, 6 Oct.2005.

**Description.** – Carapace length 3.5-5.3 mm (n=40). Rostrum (Fig. 55A; Tables 20-21) very long and slender, reaching far beyond end of scaphocerite, 1.4-2.3 times as long as carapace (n=40), armed dorsally with 9-15 teeth (including 1-3 teeth posterior to orbital margin), approx. anterior 2/3 unarmed, without subapical teeth, armed ventrally with 16-29 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.6-0.7 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.9-1.0 times as long as carapace (n=5), second segment 1.8-2.2 times length of third segment, third segment 0.3 times length of basal segment. Stylocerite reaching 0.8-0.9 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 55B) 3.6-4.5 times as long as wide (n=5).

Sixth abdominal somite 0.4-0.9 times length of carapace (n=40), 1.0-2.6 times as long as fifth somite (n=40), 1.2-1.3 times length of telson (n=5). Telson (Fig. 55E,J) 3.6-4.1 times as long as wide (n=5), distal margin rounded, without projection, with 3-4 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 2-3 pairs of spines, lateral pair distinctly longer than intermediate spines. Preanal carina (Fig. 55C) with a spine. Uropodal diaeresis (Fig. 55D) with 9-11 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobrachs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair of podobrachs on second maxilliped reduced strongly to a laminate form. Epipods only present on first two pereopods. Mouthparts as described by Cai & Wowor (2007).

Chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig.

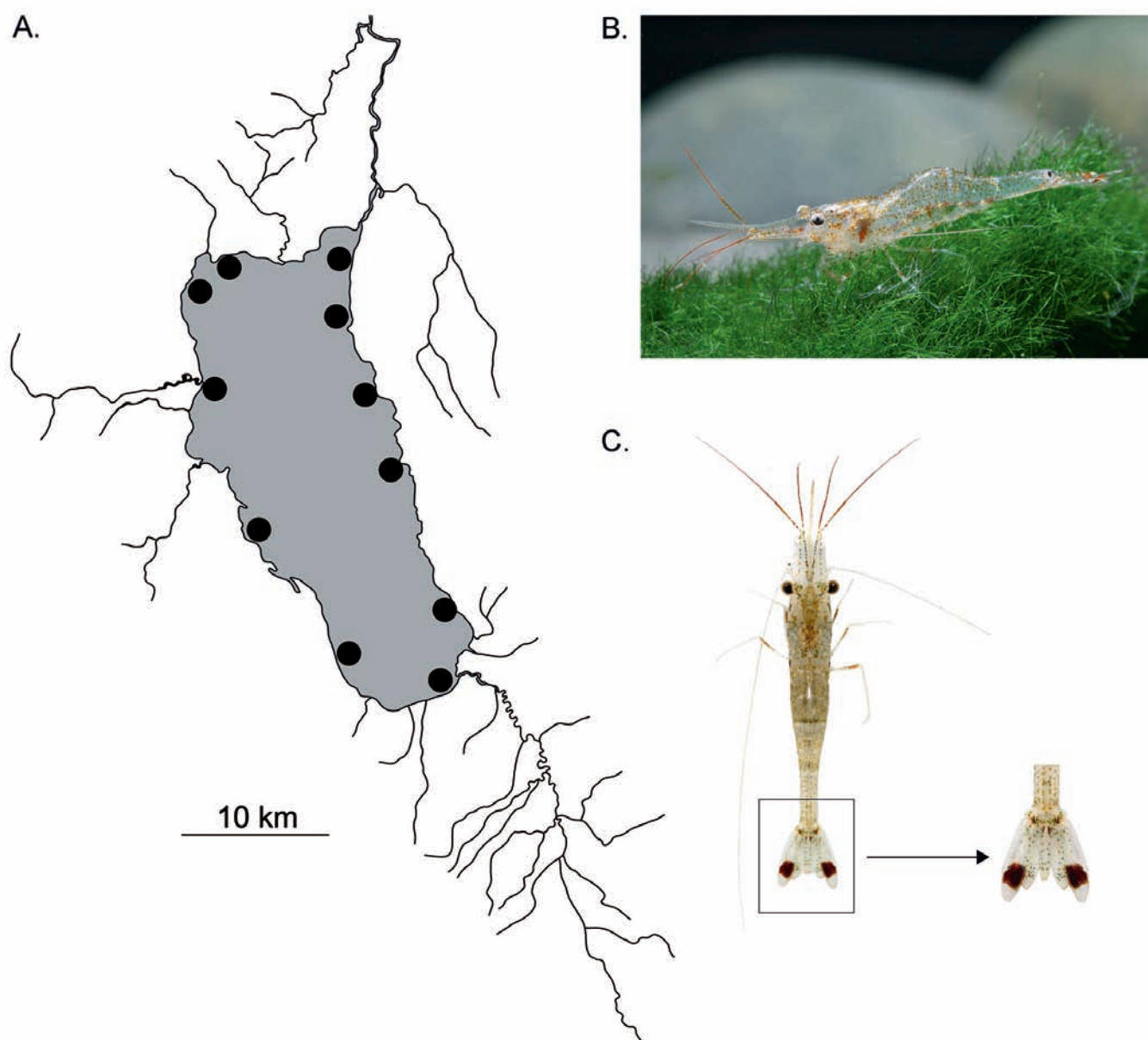


Fig. 54. *Caridina ensifera* from Lake Poso. A. Distribution. B-C. Colour pattern of living animals (not to scale). Picture B. courtesy of Chris Lukhaup.

Table 21. Summary of standard morphometric parameters for *Caridina ensifera*.

parameter	range	mean ± SD	median	n
cl (mm)	3.5-5.3	4.4 ± 0.4	4.4	40
rl / cl	1.4-2.3	2.1 ± 0.2	2.0	40
n dorsal rostral teeth	9-15	12 ± 2	12	40
n ventral rostral teeth	16-29	22 ± 3	23	40
abds6 / cl	0.4-0.9	0.9 ± 0.1	0.9	40
abds6 / abds5	1.0-2.6	2.2 ± 0.3	2.2	40
abds6 / h tel	1.2-1.3	1.2 ± 0.1	1.2	5
h tel / w tel	3.6-4.1	3.9 ± 0.2	3.9	5
n spines uropodal diaeresis	9-11	10 ± 1	10	5
h ch1 / w ch1	2.0-2.8	2.5 ± 0.2	2.5	40
h ch1 / h ca1	1.0-1.3	1.1 ± 0.1	1.1	40
h ca1 / w ca1	2.5-4.0	3.1 ± 0.4	3.2	40
h ch2 / w ch2	2.8-4.4	3.5 ± 0.3	3.4	40
h ch2 / h ca2	0.7-0.8	0.7 ± 0.0	0.7	40
h ca2 / w ca2	5.4-7.3	6.4 ± 0.5	6.4	40
n spines p3	6-9	7 ± 1	6	5
n spines p5	51-57	53 ± 3	52	5

55K-M); chela of first pereopod 2.0-2.8 times as long as wide (n=40), 1.0-1.3 times length of carpus (n=40); tips of fingers rounded, without hooks; dactylus 1.0-1.3 times as long as palm (n=5); carpus 2.5-4.0 times as long as wide (n=40), 1.0-1.3 times length of merus (n=5). Chela of second pereopod 2.8-4.4 times as long as wide (n=40), 0.7-0.8 times length of carpus (n=40); tips of fingers rounded, without hooks, dactylus 1.2-1.4 times as long as palm (n=5); carpus 5.4-7.3 times as long as wide (n=40), 1.3-1.6 times as long as merus (n=5).

Third pereopod (Fig. 55F-G) slender, dactylus 5.0-5.4 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 6-9 accessory spines on flexor margin; propodus 10.0-13.0 times as long as wide, 3.1-3.7 times as long as dactylus; carpus 4.7-6.1 times as long as wide, 0.5-0.7 times as long as propodus, 0.4-0.5 times as long as merus; merus 9.2-11.4 times as long as wide, bearing 2-4 strong, movable spines on posterior margin of outer surface.

Fifth pereopod slender (Fig. 55H-I), dactylus 5.4-7.0 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 51-57 accessory spines on flexor margin; propodus 11.1-20.7 times as long as wide, 2.5-3.0 times as long as dactylus; carpus 4.9-5.4 times as long as wide, 0.5 times as long as propodus, 0.5-0.6 times as long as merus; merus 8.8-11.1 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 55N) elongated triangular, 1.8-2.5 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 55O) 0.7-0.9 length of appendix masculina (n=5).

Ovigerous females with 19-25 eggs (n=2 females); egg size 0.9-1.0 x 0.5-0.6 mm (n=20, eggs with and without eyes).

**Distribution.** – Endemic to Lake Poso (excluding rivers) and widely distributed within the lake (Fig. 54A).

**Biology & Ecology.** – *C. ensifera* is a generalist often found in pelagic swarms or sporadically on various kinds of substrate (rocks and wood or soft substrate, for example sand or macrophytes; compare von Rintelen et al., 2007a). It is the most abundant shrimp species in Lake Poso.

**Colour pattern.** – Body yellowish-transparent with few white or darker dots, antennules reddish (Fig. 54B). The most conspicuous pattern is visible on the tailfan, each exopod bearing a red spot on the distal part (Fig. 54C).

**Taxonomic remarks.** – *C. ensifera* very closely resembles *C. caerulea*, previously listed as *C. ensifera* by Cai & Wowor (2007), but discovered as a cryptic species by von Rintelen et al. (2007a). In their revision of the Lake Poso species, Cai & Wowor (2007: 314) describe the colour of *C. ensifera* as “a single specimen from Lake Poso [...] transparent finely spectra, blue-red n-shape on brachio-stegal region, blue spot on distal exopod of uropods-conspicuous”. Thus, they describe the colour pattern of *C. caerulea*, although their data rather hint at *C. ensifera* sensu Schenkel (1902). The reason to assign *C. ensifera* (this study) to the original description of *C. ensifera*, and to describe *C. caerulea* as a new species, is mainly based on the rostrum denticulation mentioned in Schenkel’s original description (see Table 20). *C. ensifera*, as here describe, shows a high congruence with Schenkel’s data (dorsally 9-15 and ventrally 16-29 vs. dorsally 9-20 and ventrally 8-26 in the original description), whereas in *C. caerulea* the number of ventral teeth (26-48) does not really agree with Schenkel’s description, especially

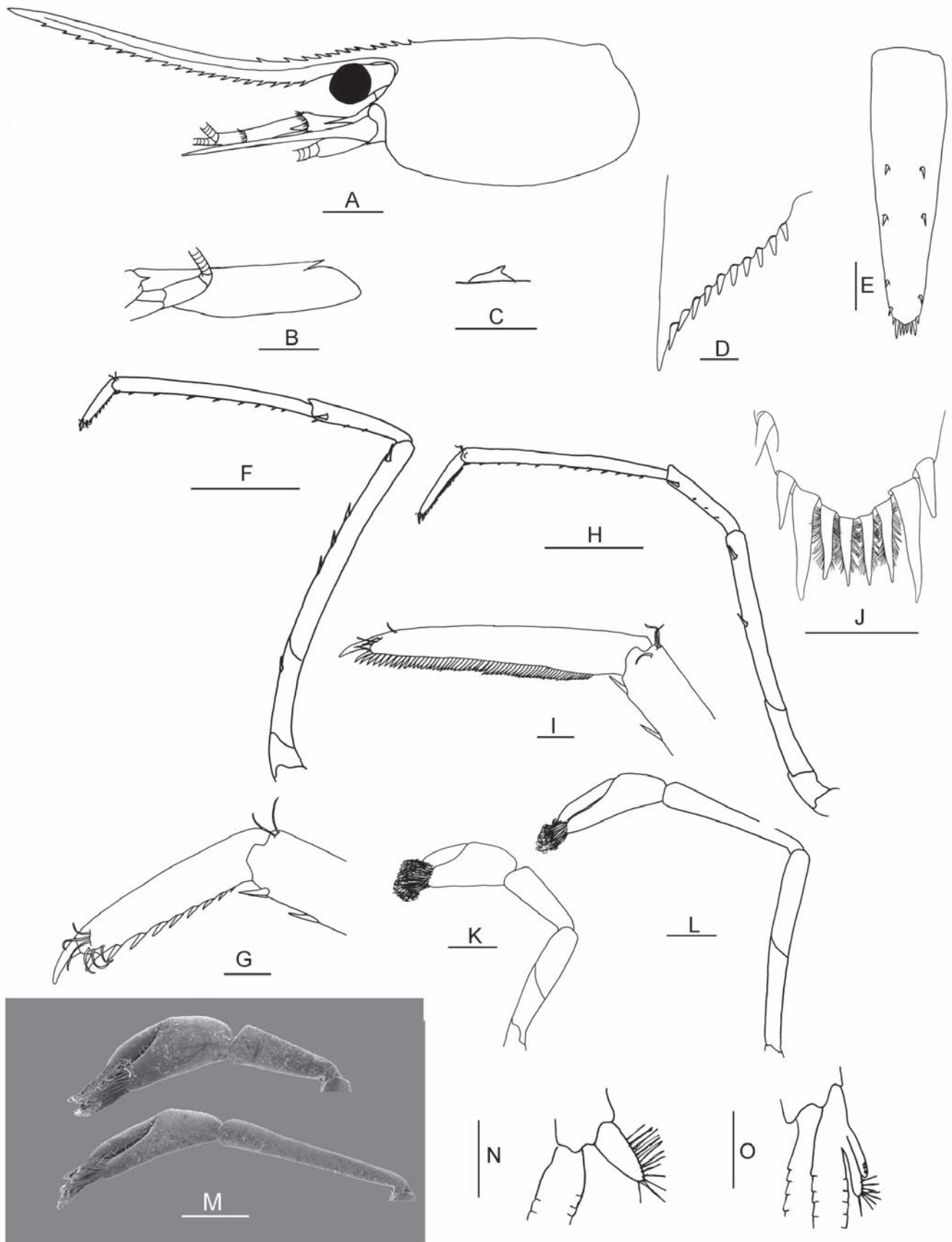


Fig. 55. *Caridina ensifera* from Lake Poso. A. Cephalothorax and cephalic appendages, female (ZMB 29389); B. Scaphocerite, male (ZMB 29404); C. Preanal carina; D. Uropodal diaeresis, female (ZMB 29389); E. Telson, female (ZMB 29248); F. Third pereiopod, female (ZMB 29389); G. Dactylus of third pereiopod; H. Fifth pereiopod; I. Dactylus of fifth pereiopod; J. Distal end of telson, female (ZMB 29248); K. First pereiopod, male (ZMB 29404); L. Second pereiopod; M. SEM image of chela and carpus of first and second pereiopods; N. Endopod of male first pleopod; O. Appendix masculina of male second pleopod. Scale bars: A-B = 1.0 mm; C, E-F, H, J-O = 0.5 mm; D, G, I = 0.1 mm.

if the median is considered. Other parameters of Schenkel's description either fit both species (for example the number of spinules and spines of the telson) or are not comparable due to an obviously different technique of measurement (for example the carapace and rostrum length). Another aspect to consider here is that *C. ensifera* generally has the highest density of all shrimps in Lake Poso and we thus assume it more likely to be caught by the Sarasins than *C. caerulea*. Although *C. ensifera* is almost identical with *C. caerulea* (not counting the always distinct colour pattern), it can not only be distinguished by a generally lower number of rostral teeth (Table 20), but also by a lower number of spines on the uropodal diaeresis (9-11 vs. 11-14 in *C. caerulea*) and by a higher number of spines on the third and fifth pereopod (6-9 and 51-57 vs. 4-5 and 27-49 in *C. caerulea*). A discriminant analysis of several morphological characters separates both species a hundred percent (von Rintelen et al. 2007a).

The morphological results are well supported by molecular data (Figs. 63,65), placing *C. ensifera* and *C. caerulea* in two separate clades that are not even sister groups (for a detailed discussion see von Rintelen et al., 2007a).

***Caridina longidigita* Cai & Wowor, 2007**  
(Figs. 56–57; Table 22)

*Caridina longidigita* Cai & Wowor, 2007: 317, Figs. 4-5 (type locality: west coast of Lake Poso at Taipa area, Poso River at the outlet of Lake Poso, east coast of Lake Poso at Besuna village).

*Caridina longidigita* – von Rintelen et al., 2008: 2244, Table 1.

*Caridina spec.* A – von Rintelen et al., 2007a: 1035, fig. 2, Tables 1-2.

**Material examined.** – Lake Poso: 42 ex. (MZB Cru 1704a, n=5; ZMB 29060a, n=6; MZB Cru 1705b, n=9; ZMB 29060b, n=12; MZB Cru 1706c, n=5; ZMB 29060c, n=5, some SEM material), east shore, south of Cape Sinampada, 02°56.25'S, 120°40.443'E, loc. 159-04, (a) on rocks in deeper water, (b) on wood, (c) on rocks in shallow water, coll. K. & T. von Rintelen, 16 Aug.2004; 14 ex. (MZB Cru 1707, n=7; ZMB 29252, n=7, some SEM material), east shore, south of Cape Tolambu, 01°57.928'S, 120°40.536'E, loc. 65-04, on rocks, coll. M. Glaubrecht & T. von Rintelen, 30 Mar.2004; 4 ex. (ZMB 29258), west shore, Cape Bancea, 01°59.023'S, 120°35.108'E, loc. 59-04, on rocks, coll. M. Glaubrecht & T. von Rintelen, 29 Mar.2004; 7 ex. (ZMB 29289), east shore, 02°0.825'S, 120°42.007'E, loc. 161-04, on wood, coll. K. von Rintelen, 16 Aug.2004; (ZMB 29293, some juveniles), east shore, 01°59.867'S, 120°41.238'E, loc. 160-04, on mixed substrate, coll. K. & T. von Rintelen, 16 Aug.2004; 1 ex. (ZMB 29387), west shore, 02°2.734'S, 120°37.368'E, loc. 178-05, on wood, coll. K. von Rintelen, 6 Oct.2005; 22 ex. (MZB Cru 1708, n=11; ZMB 29390, n=11, some SEM material), east shore, bay at Cape Nceppo, 01°52.39'S, 120°38.974'E, loc. 156-05, on mixed substrate, coll. K. von Rintelen, 3 Oct.2005; 8 ex. (ZMB 29391), east shore, at road Tentena-Peura, 01°47.33'S, 120°38.079'E, loc. 160-05, on wood, coll. K. von Rintelen, 3 Oct.2005; 5 ex. (ZMB 29398), east shore, shallow bay at Cape Songuo, 01°53.748'S, 120°39.939'E, loc. 155-05, on mixed substrate, coll. R. Lamers & K. von Rintelen, 3 Oct.2005; 3 ex. (ZMB 29401), west shore, Taipa, 01°55.289'S, 120°32.77'E, loc. 182-05, on wood, coll. K. von Rintelen, 6 Oct.2005; 1 ex. (ZMB 29456), west shore,

01°58.21'S, 120°34.316'E, loc. 181-05, on wood, coll. K. von Rintelen, 6 Oct.2005.

**Description.** – Carapace length 2.9-4.1 mm (n=12). Rostrum (Fig. 57A; Table 22) long with an anterior upturn, mostly reaching beyond end of scaphocerite, 0.9-1.4 times as long as carapace (n=11), armed dorsally with 16-21 teeth (including 4-6 teeth posterior to orbital margin), approx. anterior third to half unarmed, without subapical teeth, armed ventrally with 13-23 teeth (n=8). Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.5-0.6 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 1.0-1.1 times as long as carapace (n=5), second segment 1.5-0.2 times length of third segment, third segment 0.3-0.4 times length of basal segment. Stylocerite reaching 0.9-1.0 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 57D) 3.8-4.3 times as long as wide (n=5).

Sixth abdominal somite 0.5-0.7 times length of carapace (n=11), 1.7-1.9 times as long as fifth somite (n=10), 1.0-1.1 times length of telson (n=6). Telson (Fig. 57C,H) 2.9-3.1 times as long as wide (n=5), distal margin broadly rounded, without projection, with 3-4 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 4 pairs of spines, lateral pair longer than intermediate pairs, median pairs shortest. Preanal carina (Fig. 57E) with a spine. Uropodal diaeresis (Fig. 57B) with 15-17 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipods absent from all pereopods. Mouthparts as described by Cai & Wowor (2007).

Chela and carpus of first pereopod not distinctly stouter and broader than chela and carpus of second pereopod (Fig. 57K-N); chela of first pereopod long and slender, 4.6-6.5 times as long as wide (n=9), 0.7-1.0 times length of carpus (n=10); tips of fingers rounded, without hooks, but with extremely long fingers (about length of or longer than chela); dactylus 3.6-4.6 times as long as palm (n=5); carpus 4.8-8.1 times as long as wide (n=8), 1.0-1.2 times length of merus (n=5). Chela of second pereopod 4.8-6.4 times as long as wide (n=9), 0.7-1.0 times length of carpus (n=10); tips of fingers rounded, without hooks, but with extremely long fingers (about length of or longer than chela); dactylus 3.4-3.9 times as long as palm (n=5); carpus 5.2-7.9 times as long as wide (n=8), 1.0-1.3 times as long as merus (n=5).

Third pereopod (Fig. 57F,I) slender, dactylus 3.1-3.6 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 4-5 accessory spines on flexor margin; propodus 11.5-15.0 times as long as wide, 4.7-6.5 times as long as dactylus; carpus 6.4-8.5 times as long as wide, 0.7-0.8 times as long as propodus, 0.5-0.6 times as long as merus; merus 9.4-11.5

times as long as wide, bearing 3-5 strong, movable spines on posterior margin of outer surface.

Fifth pereopod slender (Fig. 57G,J), dactylus 2.9-3.9 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 26-33 accessory spines on flexor margin; propodus 12.9-20.0 times as long as wide, 4.6-6.7 times as long as dactylus; carpus 6.3-7.5 times as long as wide, 0.6 times as long as propodus, 0.6 times as long as merus; merus 9.1-10.2 times as long as wide, bearing 2-4 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 57O) elongated triangular, 1.9-2.3 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 57P) 0.8-0.9 times length of appendix masculina (n=5).

Ovigerous females with 24-29 eggs (n=2 females); egg size 1.0-1.2 x 0.6-0.7 mm (n=20, eggs with and without eyes).

**Distribution.** – Endemic to Lake Poso (excluding rivers) and widely distributed within the lake (Fig. 56A), although less abundant than *C. ensifera*.

**Biology and ecology.** – Cai & Wowor (2007) already mentioned the occurrence of *C. longidigita* on “rocky substrates”. This could not only be confirmed in the field, but also further differentiated in gravel from shallow water (above 3 m) and boulders in deeper water (below 3 m). Additional samples from wood show this species to be a typical hard-substrate dweller. Further, *C. longidigita* shows a unique feeding behaviour that has not been reported from any species of *Caridina* so far. Instead of the common feeding behaviour described by Fryer (1960), *C. longidigita* makes lateral sweeping movements with its extremely long fingers

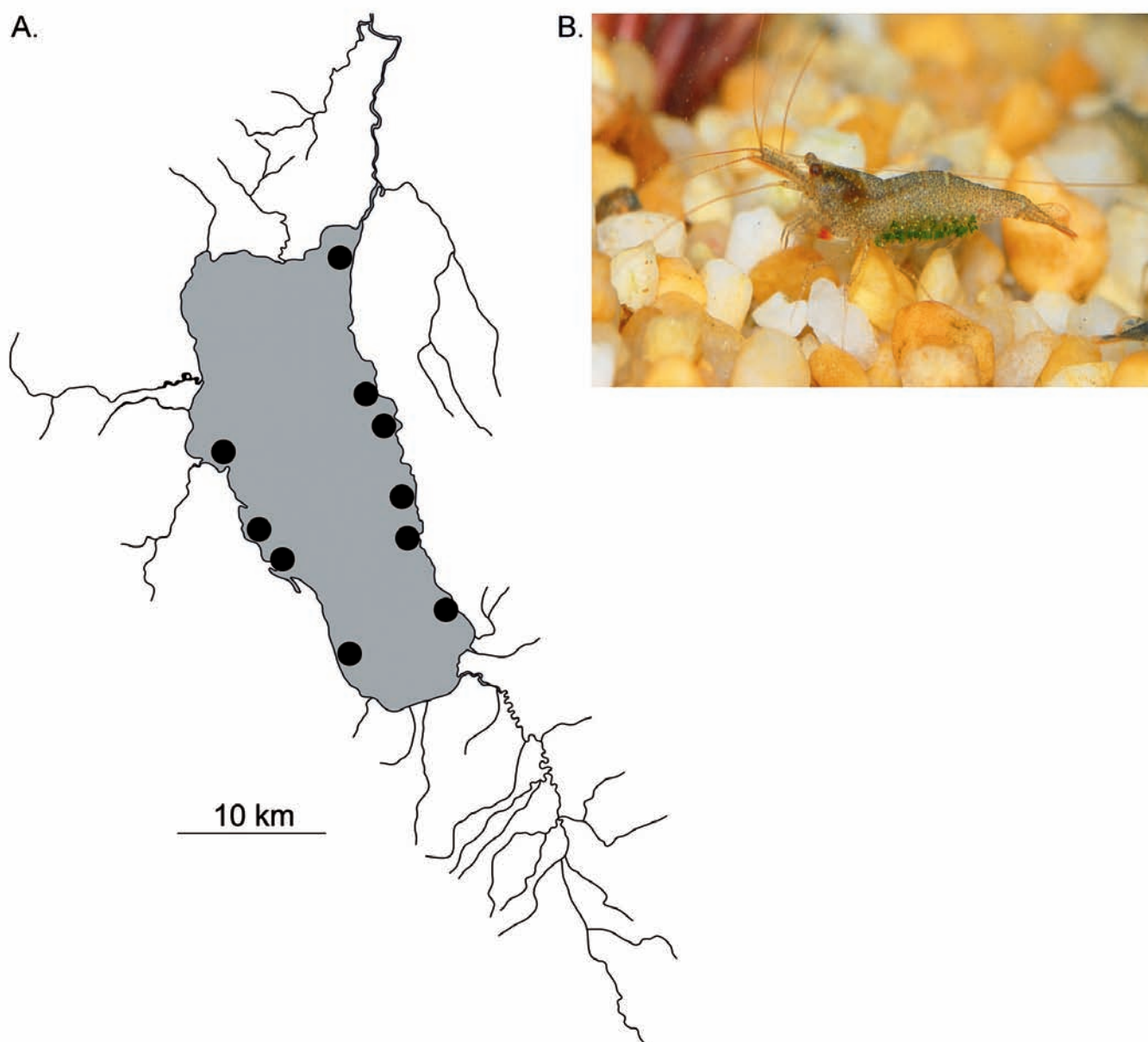


Fig. 56. *Caridina longidigita* from Lake Poso. A. Distribution. B. Colour pattern of living animal (not to scale). Picture courtesy of Chris Lukhaup.

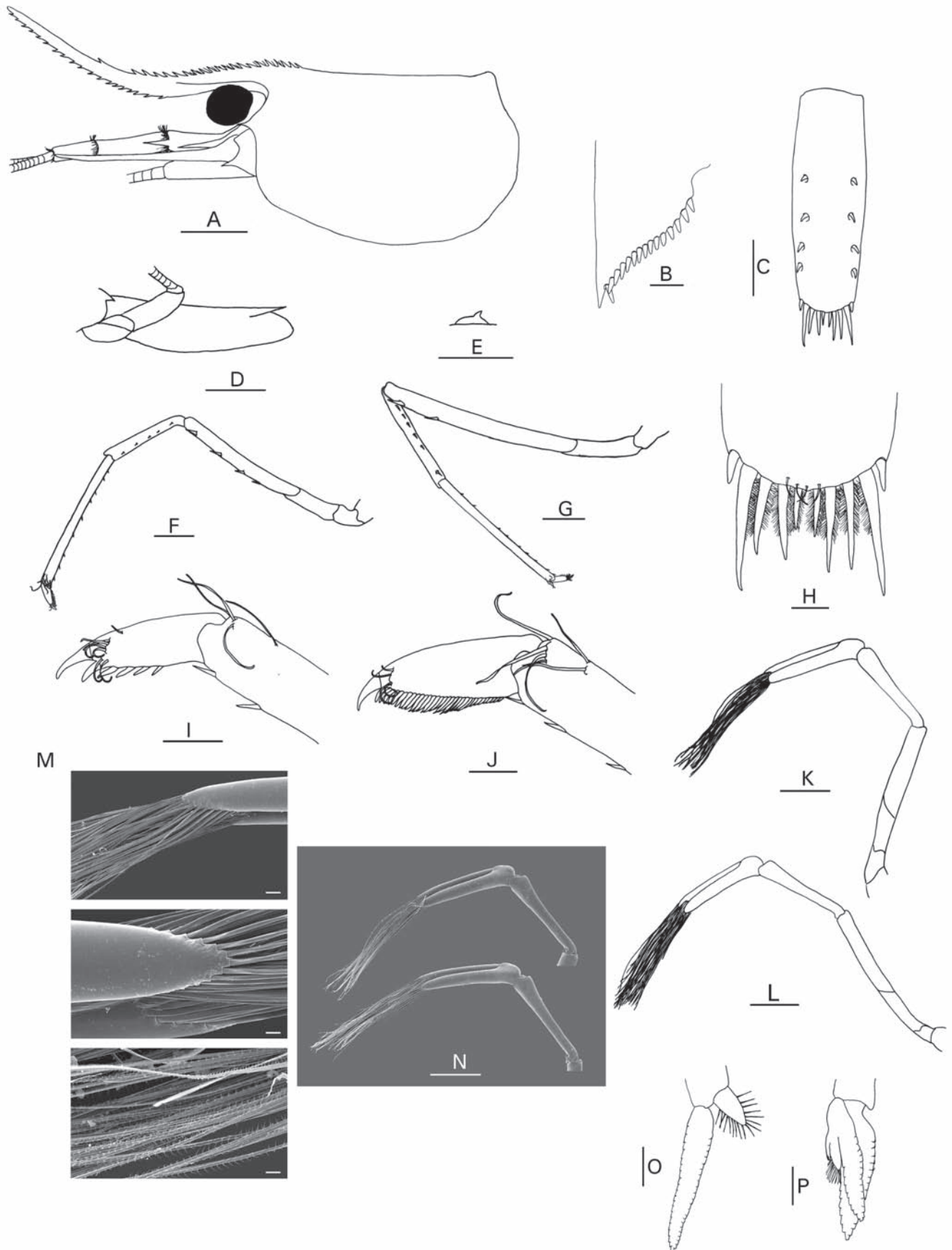


Fig. 57. *Caridina longidigita* from Lake Poso. A. Cephalothorax and cephalic appendages, male (ZMB 29252); B. Uropodal diaeresis; C. Telson; D. Scaphocerite, male (ZMB 29390); E. Preanal carina, F. Third pereiopod, male (ZMB 29252); G. Fifth pereiopod; H. Distal end of telson; I. Dactylus of third pereiopod; J. Dactylus of fifth pereiopod; K. First pereiopod, female (ZMB 29390); L. Second pereiopod; M. SEM image of anterior part of chelae (from top: lateral, ventral, setae), male (ZMB 29252); N. SEM image of chela and carpus of first and second pereiopods, male (ZMB 29390); O. Endopod of male first pleopod; P. Appendix masculina of male second pleopod. Scale bars: A, D = 1.0 mm; E-G, K-P = 0.5 mm; B, H-J = 0.1 mm.



Table 22. Summary of standard morphometric parameters for *Caridina longidigita*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	2.9-4.1	3.5 $\pm$ 0.3	3.4	12
rl / cl	0.9-1.4	1.2 $\pm$ 0.2	1.3	11
n dorsal rostral teeth	16-21	18 $\pm$ 2	18	8
n ventral rostral teeth	13-23	16 $\pm$ 4	16	8
abds6 / cl	0.5-0.7	0.6 $\pm$ 0.1	0.6	11
abds6 / abds5	1.7-1.9	1.8 $\pm$ 0.1	1.7	10
abds6 / h tel	1.0-1.1	1.0 $\pm$ 0.0	1.0	6
h tel / w tel	2.9-3.1	3.0 $\pm$ 0.1	3.0	5
n spines uropodal diaeresis	15-17	16 $\pm$ 1	16	5
h ch1 / w ch1	4.6-6.5	5.6 $\pm$ 0.5	5.6	9
h ch1 / h ca1	0.7-1.0	0.9 $\pm$ 0.1	0.9	10
h ca1 / w ca1	4.8-8.1	6.6 $\pm$ 1.1	6.7	8
h ch2 / w ch2	4.8-6.4	5.5 $\pm$ 0.5	5.5	9
h ch2 / h ca2	0.7-1.0	0.9 $\pm$ 0.1	0.8	10
h ca2 / w ca2	5.2-7.9	6.7 $\pm$ 1.1	7.1	8
n spines p3	4-5	5 $\pm$ 1	5	5
n spines p5	26-33	30 $\pm$ 3	30	5

(M. Glaubrecht & T. von Rintelen, pers. field observation 2007), while all other species lack this lateral component.

**Colour pattern.** – Body appearing transparently brownish to greenish (sometimes darker), with small dots covering the whole body. Fingers of chelae orange, but without a particular pattern (Fig. 56B). Eggs dark brown.

**Taxonomic remarks.** – *C. longidigita* mostly resembles *C. sarasinorum*, but can easily be distinguished by its extremely long fingers on the chela of the first and second pereopod (vs. short in *C. sarasinorum*) and by more slender pereopods. It differs further by a higher number of ventral rostral teeth (13-23, median 16 vs. 8-14, median 13 in *C. sarasinorum*).

In the molecular phylogeny, *C. longidigita* does not appear monophyletic (Figs. 63,65), but based on its distinctive morphology it is regarded as a single valid species that might sometimes hybridize with other species (compare von Rintelen et al., 2007a).

***Caridina sarasinorum*** Schenkel, 1902  
(Figs. 58–59; Table 23)

*Caridina sarasinorum* Schenkel, 1902: 492, pl. 8, Figs. 2a-e, 4a (type locality: Lake Poso).

*Caridina sarasinorum* – Chace, 1997: 19; Cai & Wowor, 2007: 315, fig. 3; von Rintelen et al., 2007a: 1033, fig. 2, Tables 1-2, 2008: 2244, Table 1.

*Caridina Sarasinorum* – Roux, 1904: 551; Bouvier, 1905: 73, 1913b: 182, 1925: 168, Figs. 356-359.

**Material examined.** – Lectotype: ovigerous female (cl 3.1 mm) (NHMB 2a), Indonesia, Sulawesi, Lake Poso, coll. Sarasin, no date indicated.

Paralectotypes – 4 males (cl 2.6-2.9 mm), 6 females (cl 2.7-3.4 mm) (NHMB 2a), data same as lectotype.

Others: Lake Poso: 3 ex. (ZMB 29068), south shore, Pendolo beach at Hotel Mulia, 02°3.928'S, 120°41.536'E, loc. 157-04, on wood, coll. K. & T. von Rintelen, 15 Aug.2004; 2 ex. (ZMB 29137), east shore, 01°59.867'S, 120°41.238'E, loc. 160-04, on mixed substrate, coll. K. & T. von Rintelen, 16 Aug.2004; 12 ex. (ZMB 29201a, n=6; ZMB 29201b, n=1, and MZB Cru 1732, n=5), east shore, south of Cape Sinampada, 02°56.25'S, 120°40.443'E, loc. 159-04, (ZMB a) on leaf litter, (ZMB b and MZB) on wood, coll. M. Glaubrecht & T. von Rintelen, 30Mar.2004; 7 ex. (ZMB 29261, some SEM material), east shore, Cape Watulunto, 02°0.825'S, 120°42.007'E, loc. 63-04, on leaf litter, coll. M. Glaubrecht & T. von Rintelen, 30 Mar.2004; 17 ex. (MZB Cru 1733, n=9; ZMB 29288, n=8), east shore, 02°0.825'S, 120°42.007'E, loc. 161-04, on wood, coll. K. von Rintelen, 16 Aug.2004; 13 ex. (MZB Cru 1734, n=6; ZMB 29383, n=7), west shore, Siuri, 01°48.259'S, 120°31.667'E, loc. 186-05, on mixed substrate, coll. K. von Rintelen, 6 Oct.2005; 5 ex. (ZMB 29386), west shore, 02°2.734'S, 120°37.368'E, loc. 178-05, on wood, coll. K. von Rintelen, 6 Oct.2005; 11 ex. (MZB Cru 1735, n=6; ZMB 29388, n=5, some SEM material), east shore, at road Tentena-Peura, 01°47.33'S, 120°38.079'E, loc. 160-05, on wood, coll. K. von Rintelen, 3 Oct.2005; 14 ex. (MZB Cru 1736, n=7; ZMB 29402, n=7, some SEM material), west shore, 01°52.205'S, 120°32.281'E, loc. 184-05, on macrophytes, coll. K. von Rintelen, 6 Oct.2005; 15 ex. (MZB Cru 1737, n=8; ZMB 29403, n=7), east shore, shallow bay, 01°49.702'S, 120°38.161'E, loc. 159-05, on macrophytes, coll. K. von Rintelen, 3 Oct.2005; 1 ex. (ZMB 29406), west shore, Taipa, 01°55.289'S, 120°32.77'E, loc. 182-05, on wood, coll. K. von Rintelen, 6 Oct.2005.

**Description.** – Carapace length 2.6-3.6 mm (n=12). Rostrum (Fig. 59A; Table 23) long, reaching beyond end of scaphocerite, 1.0-1.2 times as long as carapace (n=8), armed dorsally with 15-21 teeth (including 4-6 teeth posterior to orbital margin), approx. anterior third to half unarmed, without subapical teeth, armed ventrally with 8-14 teeth. Antennal spine situated below inferior orbital

Table 23. Summary of standard morphometric parameters for *Caridina sarasinorum*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	2.6-3.6	3.1 $\pm$ 0.3	3.1	12
rl / cl	1.0-1.2	1.1 $\pm$ 0.1	1.1	8
n dorsal rostral teeth	15-21	18 $\pm$ 2	17	8
n ventral rostral teeth	8-14	12 $\pm$ 2	13	8
abds6 / cl	0.6-0.8	0.7 $\pm$ 0.1	0.7	11
abds6 / abds5	1.7-2.0	1.9 $\pm$ 0.1	1.9	11
abds6 / h tel	0.9-1.0	0.9 $\pm$ 0.1	1.0	6
h tel / w tel	3.2-3.6	3.4 $\pm$ 0.2	3.3	5
n spines uropodal diaeresis	8-10	9 $\pm$ 1	9	5
h ch1 / w ch1	1.9-2.0	1.9 $\pm$ 0.1	1.9	8
h ch1 / h ca1	1.3-1.5	1.5 $\pm$ 0.1	1.5	9
h ca1 / w ca1	1.1-1.9	1.7 $\pm$ 0.3	1.7	8
h ch2 / w ch2	2.2-2.9	2.5 $\pm$ 0.2	2.6	8
h ch2 / h ca2	0.8-0.9	0.8 $\pm$ 0.1	0.8	9
h ca2 / w ca2	3.6-5.0	4.4 $\pm$ 0.5	4.6	8
n spines p3	6-7	7 $\pm$ 0	7	5
n spines p5	33-43	39 $\pm$ 4	39	5

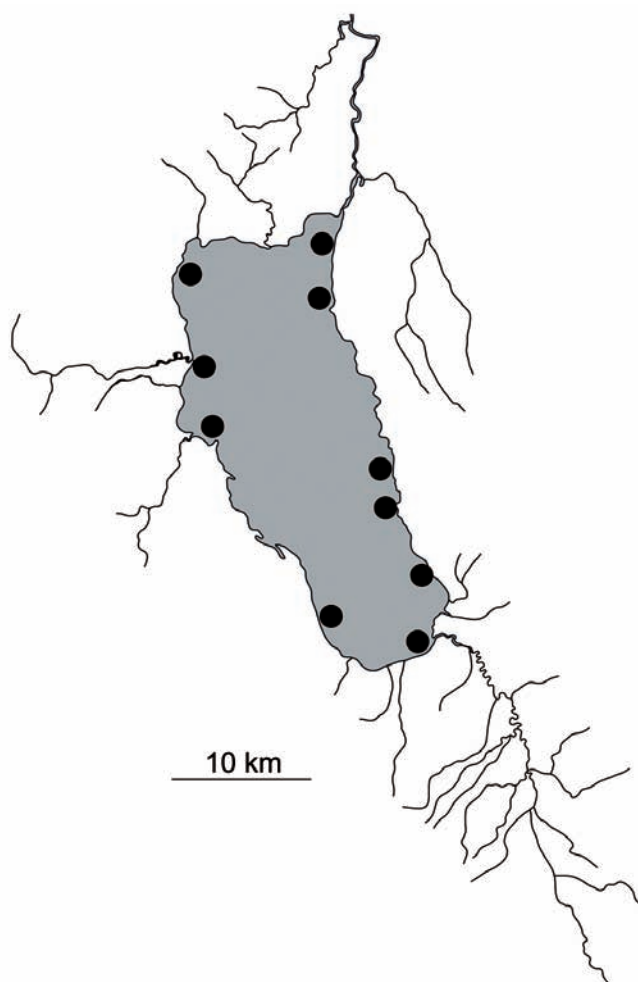


Fig. 58. Distribution of *Caridina sarasinorum* in Lake Poso.

angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.5-0.6 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.9-1.1 times as long as carapace (n=5), second segment 1.7-2.0 times length of third segment, third segment 0.3-0.4 times length of basal segment. Stylocerite reaching 0.9-1.0 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 59D) 3.8-4.4 times as long as wide (n=5).

Sixth abdominal somite 0.6-0.8 times length of carapace (n=11), 1.7-2.0 times as long as fifth somite (n=11), 0.9-1.0 times length of telson (n=6). Telson (Fig. 59C,H,K) 3.2-3.6 times as long as wide (n=5), distal margin rounded, without projection, with 3-4 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 3 pairs of spines, lateral pair sometimes but not always longer than intermediate pairs. Preanal carina (Fig. 59E) with a spine. Uropodal diaeresis (Fig. 59B) with 8-10 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipods present on first pereopod, greatly reduced or absent from second pereopod. Mouthparts as described by Cai & Wowor (2007).

Chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig. 59L-N); chela of first pereopod 1.9-2.0 times as long as wide (n=8), 1.3-1.5 times length of carpus (n=9); tips of fingers rounded, without hooks; dactylus 0.9-1.1 times as long as palm (n=5); carpus 1.1-1.9 times as long as wide (n=8), 1.0-1.2 times length of merus (n=5). Chela of second pereopod 2.2-2.9 times as long as wide (n=8), 0.8-0.9 times

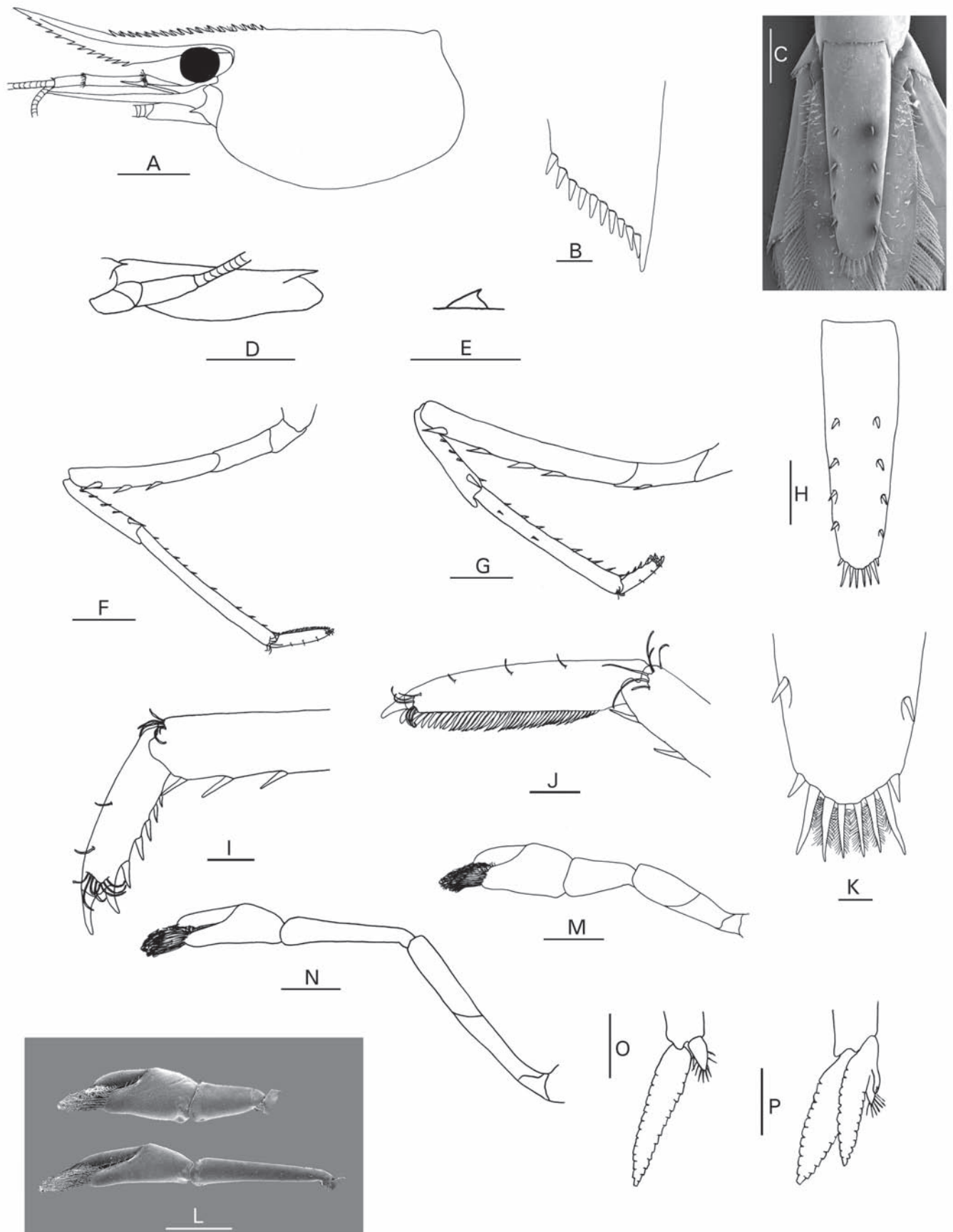


Fig. 59. *Caridina sarasinorum* from Lake Poso. A. Cephalothorax and cephalic appendages, female (ZMB 29388); B. Uropodal diaeresis, male (ZMB 29402); C. SEM image of telson and uropods, female (ZMB 29388); D. Scaphocerite, female (ZMB 29403); E. Preanal carina; F. Fifth pereiopod, female (ZMB 29388); G. Third pereiopod; H. Telson; I. Dactylus of third pereiopod; J. Dactylus of fifth pereiopod; K. Distal end of telson; L. SEM image of chela and carpus of first and second pereiopods; M. First pereiopod; N. Second pereiopod; O. Endopod of male first pleopod (ZMB 29403); P. Appendix masculina of male second pleopod. Scale bars: A, D = 1.0 mm; C, E-H, L-P = 0.5 mm; B, I-K = 0.1 mm.

length of carpus (n=9); tips of fingers rounded, without hooks, dactylus 0.9-1.4 times as long as palm (n=5); carpus 3.6-5.0 times as long as wide (n=8), 1.3-1.5 times as long as merus (n=5).

Third pereopod (Fig. 59G,I) slender, dactylus 3.3-4.5 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 6-7 accessory spines on flexor margin; propodus 9.3-11.7 times as long as wide, 2.9-4.1 times as long as dactylus; carpus 4.1-5.0 times as long as wide, 0.6-0.7 times as long as propodus, 0.5-0.6 times as long as merus; merus 6.8-8.9 times as long as wide, bearing 3-4 strong, movable spines on posterior margin of outer surface.

Fifth pereopod slender (Fig. 59F,J), dactylus 4.0-5.6 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 33-43 accessory spines on flexor margin; propodus 10.0-16.0 times as long as wide, 2.6-3.2 times as long as dactylus; carpus 4.3-5.7 times as long as wide, 0.5-0.6 times as long as propodus, 0.6 times as long as merus; merus 6.3-7.8 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 59O) elongated triangular, 1.9-2.5 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 59P) 0.8-0.9 times length of appendix masculina (n=5).

Ovigerous females with 19-23 eggs (n=2 females); egg size 0.9-1.0 x 0.5-0.6 mm (n=20, eggs with and without eyes).

**Distribution.** – Endemic to Lake Poso (excluding rivers), widely distributed within the lake (Fig. 58), although less abundant than *C. ensifera*.

**Biology and ecology.** – *C. sarasinorum* was found on various kinds of substrate (wood, leaf litter, macrophytes), particularly on weed and wood, often in large numbers at several localities.

**Colour pattern.** – Body transparently yellowish or greenish, lacking a particular pattern. However, further details are still unknown.

**Taxonomic remarks.** – *C. sarasinorum* resembles *C. longidigita*, but can easily be distinguished by its stouter pereopods and the short fingers on the chela of the first and second pereopod (vs. distinctly more slender pereopods and very long fingers in *C. longidigita*). It further differs by a lower number of ventral rostral teeth (8-14, median 13 vs. 13-23, median 16 in *C. longidigita*).

In the molecular phylogeny (Figs. 63,65), *C. sarasinorum* does not appear monophyletic, but based on its distinctive morphology it is here regarded as a single valid species that might sometimes hybridize with other species (compare von Rintelen et al., 2007a).

### *Caridina schenkeli*, new species

(Figs. 60–62; Table 24)

*Caridina spec.* B – von Rintelen et al., 2007a: 1035, fig. 2, Tables 1-2.

**Material examined.** – Holotype: female (cl 4.3 mm)(MZB Cru 2124), small stream, west of Lake Poso, 02°2.613'S, 120°37.311'E, loc. 179-05, on macrophytes, coll. K. von Rintelen, 6 Oct.2005.

Paratypes (Lake Poso catchment) – 38 ex. (MZB Cru 1724, n=19; ZMB 29159, n=19), Uebangke River, north of tributary of Lake Poso, 01°46.48'S, 120°35.61'E, loc. 188-05, on mixed substrate, coll. K. von Rintelen, 7 Oct.2005; 24 ex. (MZB Cru 1725, n=12; ZMB 29254, n=12), Sulewana, above rapids, 01°39.121'S, 120°39.742'E, loc. 52-04, on mixed substrate, coll. M. Glaubrecht & T. von Rintelen, 28 Mar.2004; 22 ex. (MZB Cru 1726, n=11; ZMB 29407, n=11), Njongi River, approx. 1 km east of Tentena, 01°44.348'S, 120°40.102'E, loc. 163-05, on macrophytes, coll. K. & T. von Rintelen, 3 Oct.2005; 10 ex. (ZMB 29441), small stream, west of Lake Poso, 01°53.816'S, 120°31.466'E, loc. 183-05, on roots, coll. K. von Rintelen, 6 Oct.2005; 43 ex. (MZB Cru 1727, n=22; ZMB 29442, n=21 and few juveniles, some SEM material), small stream, west of Lake Poso, 02°2.613'S, 120°37.311'E, loc. 179-05, on macrophytes, coll. K. von Rintelen, 6 Oct.2005; 11 ex. (MZB Cru 1728, n=5; ZMB 29443, n=6), stream, west of Lake Poso, 02°0.233'S, 120°35.765'E, loc. 180-05, mixed substrate, coll. K. von Rintelen, 6 Oct.2005; 25 ex. (MZB Cru 1729, n=12; ZMB 29444, n=13), Salopa River, 01°46.333'S, 120°32.49'E, loc. 177-05,

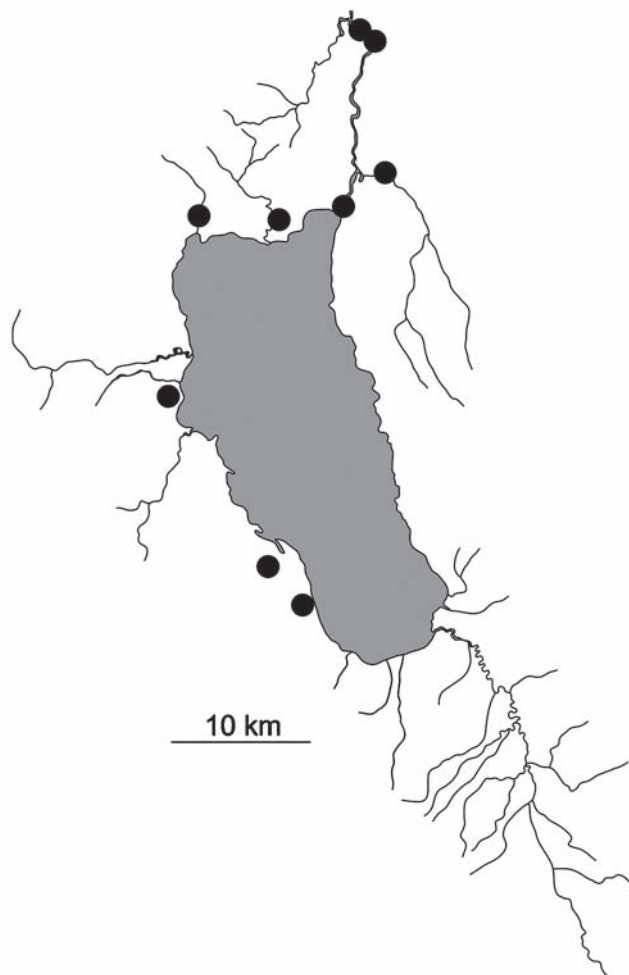


Fig. 60. Distribution of *Caridina schenkeli* in the Poso catchment.

Table 24. Summary of standard morphometric parameters for *Caridina schenkeli*.

parameter	range	mean $\pm$ SD	median	n
cl (mm)	3.6-5.1	4.2 $\pm$ 0.4	4.2	17
rl / cl	0.9-1.1	1.0 $\pm$ 0.1	0.9	10
n dorsal rostral teeth	9-16	13 $\pm$ 2	13	10
n ventral rostral teeth	9-13	11 $\pm$ 1	11	10
abds6 / cl	0.6-0.7	0.7 $\pm$ 0.0	0.7	17
abds6 / abds5	1.9-2.0	2.0 $\pm$ 0.1	2.0	6
abds6 / h tel	0.8-1.0	1.0 $\pm$ 0.1	1.0	8
h tel / w tel	3.0-3.6	3.4 $\pm$ 0.3	3.6	5
n spines uropodal diaeresis	10-11	10 $\pm$ 0	10	5
h ch1 / w ch1	1.9-3.2	2.4 $\pm$ 0.4	2.3	10
h ch1 / h ca1	1.1-1.4	1.3 $\pm$ 0.1	1.3	10
h ca1 / w ca1	2.1-3.2	2.5 $\pm$ 0.4	2.4	10
h ch2 / w ch2	2.5-4.4	3.3 $\pm$ 0.5	3.3	10
h ch2 / h ca2	0.7-0.9	0.8 $\pm$ 0.0	0.8	10
h ca2 / w ca2	4.5-6.5	5.5 $\pm$ 0.6	5.5	10
n spines p3	6-8	7 $\pm$ 1	7	5
n spines p5	57-64	59 $\pm$ 3	57	5

on mixed substrate, coll. K. & T. von Rintelen, 5 Oct.2005; 28 ex. (MZB Cru 1730, n=14; ZMB 29445, n=14, some SEM material), Sulewana, above rapids, 01°39.121'S, 120°39.742'E, loc. 169-05, on mixed substrate, coll. K. & T. von Rintelen, 4 Oct.2005; 34 ex. (MZB Cru 1731, n=17; ZMB 29446, n=17), Poso outlet, Tentena, 01°45.908'S, 120°38.366'E, loc. 195-05, on wood, coll. R. Lamers & K. von Rintelen, 7 Oct.2005; 4 ex. (ZMB 29457), Sulewana rapids, 02°38.871'S, 120°39.279'E, loc. 170-05, on macrophytes, coll. K. & T. von Rintelen, 4 Oct.2005.

**Description.** –Carapace length 3.6-5.1 mm (n=17). Rostrum (Fig. 61A; Table 24) reaching near or beyond end of scaphocerite, 0.9-1.1 times as long as carapace (n=10), armed dorsally with 9-16 teeth (including 2-5 teeth posterior to orbital margin), approx. anterior third to half unarmed, without subapical teeth, armed ventrally with 9-13 teeth. Antennal spine situated below inferior orbital angle. Pterygostomial angle broadly rounded. Eyes well developed, anterior end 0.4-0.6 times length of basal segment of antennular peduncle (n=5). Antennular peduncle 0.8-1.0 times as long as carapace (n=5), second segment 1.6-2.0 times length of third segment, third segment 0.3-0.4 times length of basal segment. Stylocerite reaching 1.0 times length of basal segment of antennular peduncle (n=5). Scaphocerite (Fig. 61D) 3.3-4.7 times as long as wide (n=5).

Sixth abdominal somite 0.6-0.7 times length of carapace (n=17), 1.9-2.0 times as long as fifth somite (n=6), 0.8-1.0 times length of telson (n=8). Telson (Fig. 61C,H) 3.0-3.6 times as long as wide (n=5), distal margin rounded, without projection, with 3-6 pairs of spinules and 1 pair of dorsolateral spinules; distal end with 2-3 pairs of spines, lateral pair usually longer than intermediate pairs. Preanal carina (Fig. 61E) with a spine. Uropodal diaeresis (Fig. 61B) with 10-11 movable spinules (n=5).

5 pairs of pleurobranchs well developed; 3 pairs of arthrobranchs, 2 on third maxillipeds, with second pair strongly reduced in size, 1 pair on first pereopod; 1 pair of podobranchs on second maxilliped reduced strongly to a laminate form. Epipod present on first two pereopods. Incisor process of mandible (Fig. 62A) ending in a row of 4-6 small teeth, molar process truncated. Lower lacinia of maxillula (Fig. 62B) broadly rounded, upper lacinia elongate, with numerous distinct teeth and setae on inner margin, palp slender. Upper endites of maxilla (Fig. 62C) subdivided, palp short, scaphognathite tapering posteriorly with numerous long, curved setae at posterior end. Distal end of palp of first maxilliped (Fig. 62F) triangular, not ending with a finger-like projection; flagellum of the exopod short, endopod high, reaching near to end of flagellum of exopod. Second maxilliped (Fig. 62E) typical. Third maxilliped (Fig. 62D) with ultimate segment as long as penultimate segment.

Chela and carpus of first pereopod distinctly stouter and broader than chela and carpus of second pereopod (Fig. 61M-O); chela of first pereopod 1.9-3.2 times as long as wide (n=10), 1.1-1.4 times length of carpus (n=10); tips of fingers rounded, without hooks; dactylus 1.0-1.4 times as long as palm (n=5); carpus 2.1-3.2 times as long as wide (n=10), 1.1-1.2 times length of merus (n=5). Chela of second pereopod 2.5-4.4 times as long as wide (n=10), 0.7-0.9 times length of carpus (n=10); tips of fingers rounded, without hooks, dactylus 1.2-1.4 times as long as palm (n=5); carpus 4.5-6.5 times as long as wide (n=10), 1.3-1.4 times as long as merus (n=5).

Dactylus of third pereopod (Fig. 61F,I) 3.3-4.3 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 6-8 accessory spines on flexor margin; propodus 9.8-14.2

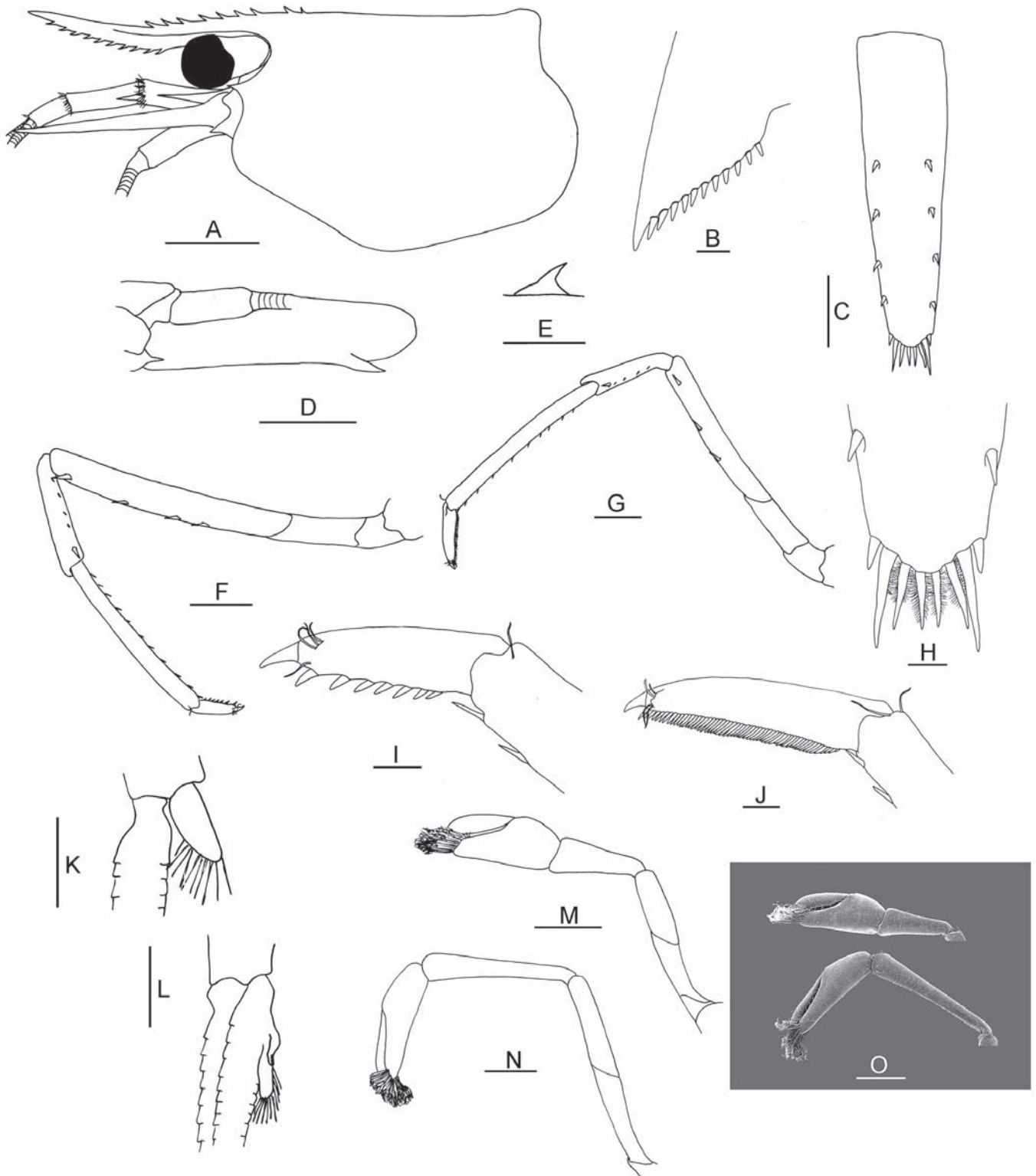


Fig. 61. *Caridina schenkeli* from the Poso catchment. A. Cephalothorax and cephalic appendages, female (ZMB 29442); B. Uropodal diaeresis; C. Telson; D. Scaphocerite; E. Preanal carina; F. Third pereiopod; G. Fifth pereiopod; H. Distal end of telson; I. Dactylus of third pereiopod; J. Dactylus of fifth pereiopod; K. Endopod of male first pleopod (ZMB 29442); L. Appendix masculina of male second pleopod; M. First pereiopod, female (ZMB 29442); N. Second pereiopod; O. SEM image of chela and carpus of first and second pereiopods. Scale bars: A, D = 1.0 mm; C, E-G, K-O = 0.5 mm; B, H-J = 0.1 mm.

times as long as wide, 3.4-4.8 times as long as dactylus; carpus 5.0-6.0 times as long as wide, 0.5-0.7 times as long as propodus, 0.5 times as long as merus; merus 8.5-10.5 times as long as wide, bearing 3-4 strong, movable spines on posterior margin of outer surface.

Dactylus of fifth pereopod (Fig. 61G,J) 3.7-4.8 times as long as wide (terminal spine included, without spines of flexor margin; n=5), terminating in one large claw with 57-64 accessory spines on flexor margin; propodus 11.5-17.0 times as long as wide, 2.8-4.5 times as long as dactylus; carpus 4.5-7.0 times as long as wide, 0.5 times as long as

propodus, 0.6-0.7 times as long as merus; merus 7.2-9.3 times as long as wide, bearing 2-3 strong, movable spines on posterior margin of outer surface.

Endopod of male first pleopod (Fig. 61K) elongated triangular, 2.0-2.4 times as long as proximally wide (n=5), without appendix interna. Appendix interna of male second pleopod (Fig. 56L) 0.7-0.8 times length of appendix masculina (n=5).

Ovigerous females with 26-37 eggs (n=2 females); egg size 1.0-1.1 x 0.6-0.7 mm (n=30, eggs with and without eyes).

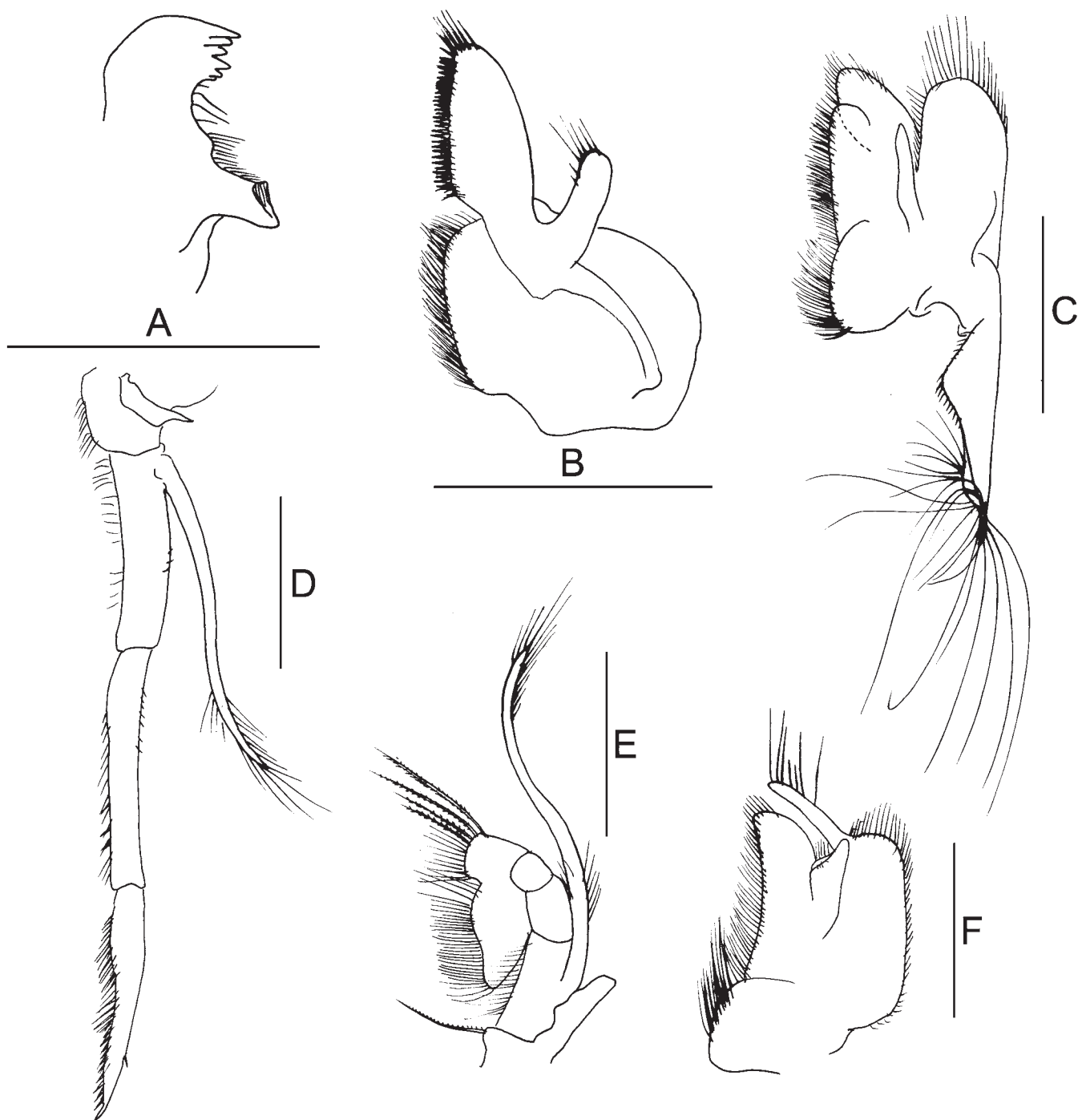


Fig. 62. *Caridina schenkeli* from the Poso catchment. A. Mandible (ZMB 29442); B. Maxillula; C. Maxilla; D. third maxilliped; E. second maxilliped; F. first maxilliped. Scale bars: A-F = 1mm.

**Distribution.** – *C. schenkeli* is endemic to the Poso catchment, but does not occur in the lake itself (Fig. 60). So far, this species has not been found in rivers east and south of Lake Poso.

**Biology and ecology.** – *C. schenkeli* is an exclusively riverine species collected from various kinds of substrate (rocks, riverine vegetation, roots, dead wood). It was not found in sympatry with the other riverine species endemic to the Poso system (*C. acutirostris*).

**Colour pattern.** – Without any species specific pattern. Body colouration transparently yellowish or brownish, typical for many other riverine species from all over Sulawesi. Large (often ovigerous) females usually appear darker than smaller specimens.

**Taxonomic remarks.** – With regard to rostrum shape and body size, *C. schenkeli* resembles *C. acutirostris* (carapace length in mm 3.6–5.1, median 4.2 and 3.1–5.8, median 4.1 in *C. acutirostris*), but differs by the ratio of rostrum to carapace length (0.9–1.1, median 0.9 vs. 0.3–0.7, median 0.5 in *C. acutirostris*), a generally longer rostrum (reaching near or beyond end of scaphocerite vs. shorter in *C. acutirostris*), and a higher number of ventral rostral teeth (9–13, median 11 vs. 4–9, median 4 in *C. acutirostris*).

*C. schenkeli* is morphologically more variable than all other Poso species. In the molecular phylogeny (Figs. 63,65), *C. schenkeli* does not appear monophyletic, but based on its distinctive morphology it is here regarded as a single valid species that might sometimes hybridize with other species (compare von Rintelen et al., 2007a).

## DISCUSSION

### Radiation, ecology, and species diversity of freshwater shrimps in the ancient lakes of Sulawesi

Von Rintelen et al. (in review) suggested at least three independent colonization events for the ancient lakes of Sulawesi, one for Lake Poso and two for the Malili lakes (compare Fig. 63). However, only one of the Malili invasions led to a subsequent radiation (von Rintelen et al., in review). Contrary to Woltereck's (1937a, b) assumption, all lacustrine species in the Malili system are endemic. Beyond these, the entire Malili species flock (i.e. including the riverine species of the lakes' catchment) is endemic to the Malili system, except for *C. mahalona*. A single specimen of that species was caught in the southernmost part of the Tomori area just north of Lake Matano (Figs. 1C). Previous studies on the ecology of the ancient lake species (Zitzler & Cai, 2006; von Rintelen et al. 2007a, b, in review) suggested the existence of substrate specialists and generalists in both species flocks. These results are confirmed in this paper and summarized for all species in Table 1. This revision, and the results gained by von Rintelen et al. (2007a, in review), reveal that the total number of species is almost twice as high than previously described (Table 2). In general, there are

conspicuously less species in Lake Poso than in the Malili lakes. The considerably lower number of taxa in Lake Poso might be explained by several factors, e.g. differences in age of the lake species flocks or the less pronounced geographical structure of Lake Poso as a single lake. Although, these hypotheses would need testing.

The molecular phylogeny (Figs. 63–65) was used to discuss the morphology-based species description. Here, we discuss the general results (compare von Rintelen et al., 2007a, b, in review): the majority of species (particularly the colourful specialists from the Malili lakes) appear monophyletic in the tree, but almost half of the morpho-species appear para- or polyphyletic. Based on our morphological results, we regard those species that do not appear monophyletic in the tree as valid species. Nevertheless, the occasional mismatch of morphological and molecular data requires an explanation: Among the lacustrine generalists (Table 1), only *Caridina lanceolata* from the Malili lakes (Figs. 63–64) and *C. ensifera* from Lake Poso (Fig. 65) are recovered as monophyletic, while the riverine generalists *C. masapi*, *C. mahalona* (Malili), and *C. schenkeli* (Poso) appear in more than one clade (Figs. 64–65). In *C. masapi* and *C. mahalona*, the existence of cryptic species seems most likely as the different clades of both species form geographic clusters (allopatric distribution; compare von Rintelen et al., in review). Von Rintelen et al. (2007a) discussed the non-monophyly of *C. schenkeli* (there *C. spec. B*) as indicative of introgressive hybridization, because the lack of distinctive colour patterns might facilitate 'mating errors' in this taxon. A similar scenario was suggested by the same authors for the lacustrine species *C. longidigita* and *C. sarasinorum* from Lake Poso. In contrast, the always distinctive and species-specific colour patterns of *C. ensifera*, *C. caerulea* (Poso), and of the majority of the colourful specialists from the Malili lake system (Table 1) seem to prevent hybridization. The molecular phylogeny further shows that the specialized lacustrine species *C. holthuisi* from the Malili lakes also appears in two geographically distinct clades (Fig. 64) that are not sister groups to each other. Hence, the genetic data (albeit the current lack of morphological differences between representatives of both clades) rather suggest the existence of two cryptic species than hybridization or incomplete lineage sorting. The only genetically (and partly morphologically, if the colour patterns in living animals is ignored) completely unresolved clade of specialists from the Malili lakes comprises the sponge-dweller *C. spongicola* and the morphologically almost indistinguishable rock-dwellers *C. glaubrechtii*, *C. striata*, and *C. woltereckae* (Fig. 64, compare von Rintelen et al. 2007b). This insufficient resolution, with basically no geographical pattern, might be caused by incomplete lineage sorting due to very recent speciation events, introgression, or the misinterpretation of intraspecific polymorphism as different species. In the first case, a better resolution might be gained with certain nuclear markers (e.g. AFLPs), which would also serve to test the other hypotheses. It is here regarded as rather unlikely that the four taxa are just intraspecific colour variants, as they also exhibit considerable differences in behaviour, particularly the widespread *C. striata* and *C. woltereckae*. These species also differ in their



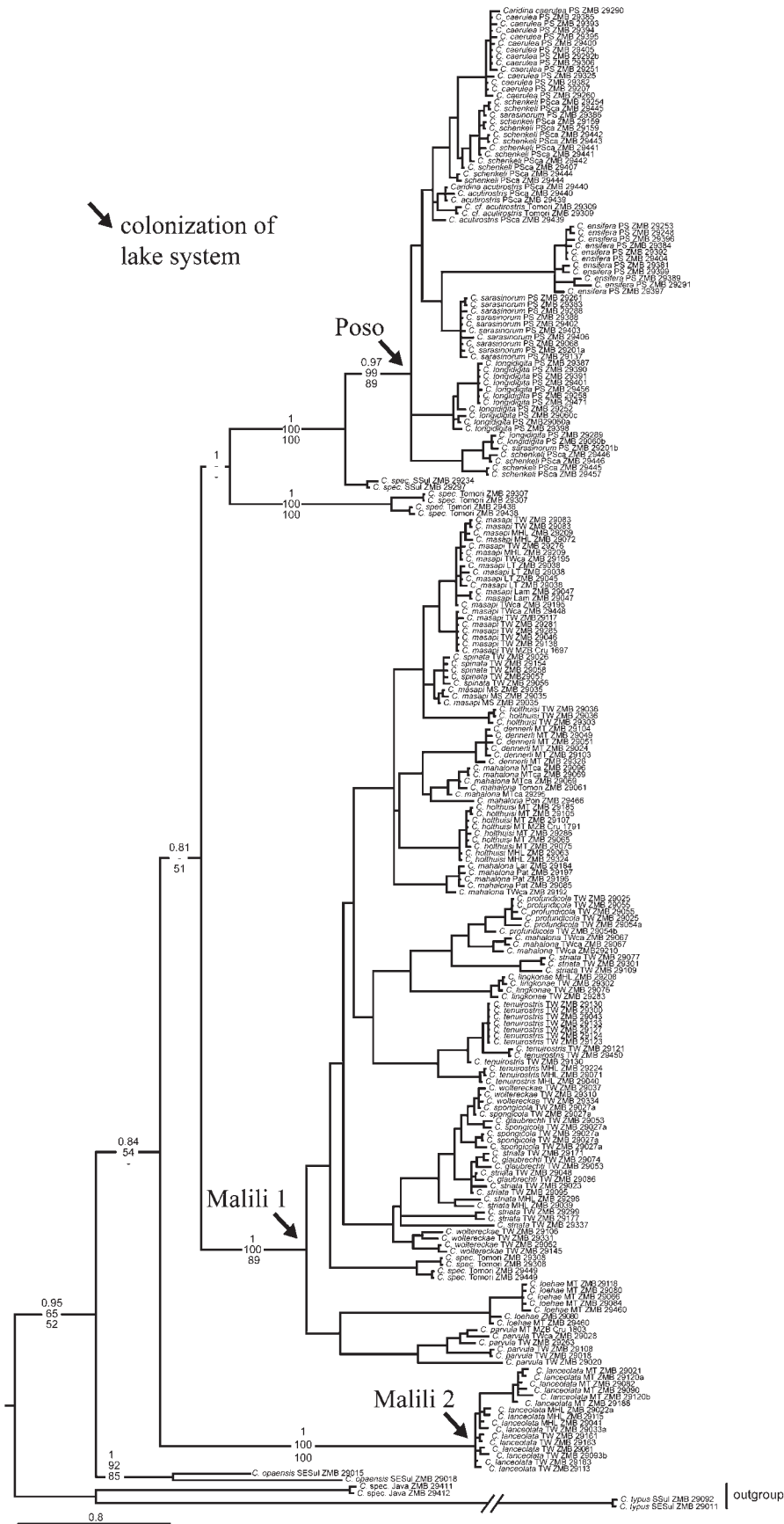


Fig. 63. Bayesian Inference phylogram (mtDNA, 16S and COI) of *Caridina* from the ancient lakes of Sulawesi (for other taxa compare von Rintelen et al., in review). Numbers on branches are, from top, Bayesian posterior probabilities, ML and MP bootstrap values. The scale bar indicates the number of substitutions per site. For each sequenced specimen museum accession numbers are provided. Locality abbreviations (compare Fig. 1): Lam (Lampesue River catchment), LT (Lake Lontoa), MHL (Lake Mahalona), MS (Lake Masapi), MT (Lake Matano), MTca (Lake Matano catchment), Pat (Patingko River), Pon (Ponsoa River), TW (Lake Towuti), TWca (Lake Towuti catchment), PS (Lake Poso), PSCa (Lake Poso catchment), SSul (South Sulawesi), SESul (Southeast Sulawesi).

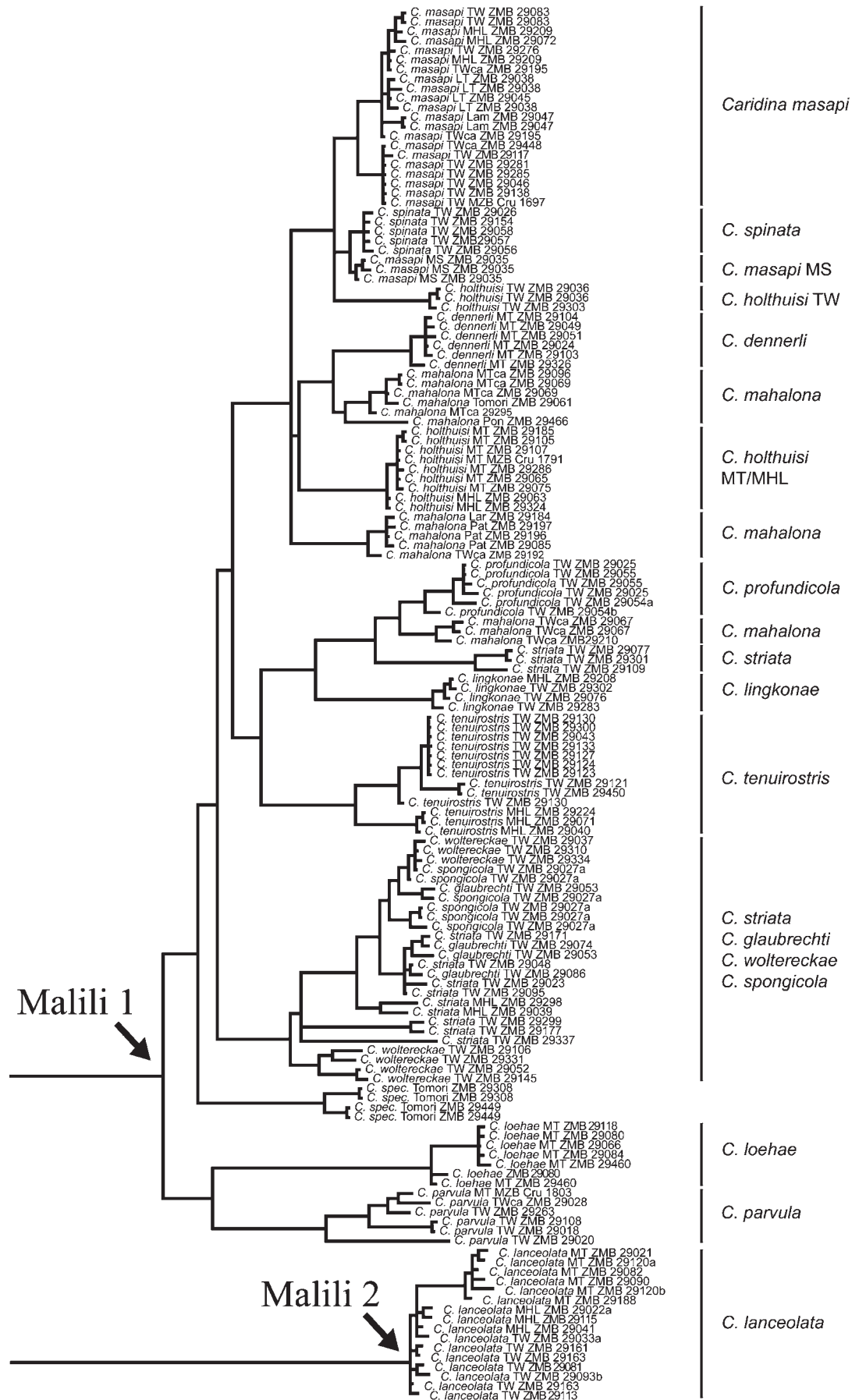


Fig. 64. Bayesian Inference phylogram (mtDNA, 16S and COI) showing taxa within the two Malili clades (for other taxa compare von Rintelen et al., 2009). For each sequenced specimen museum accession numbers are provided. Locality abbreviations (compare Fig. 1): Lam (Lampesue River catchment), LT (Lake Lontoa), MHL (Lake Mahalona), MS (Lake Masapi), MT (Lake Matano), MTca (Lake Matano catchment), Pat (Patingko River), Pon (Ponsoa River), TW (Lake Towuti), TWca (Lake Towuti catchment), SSul (South Sulawesi).

use of the same substrate, and *C. spongicola* is not a rock dweller at all. In a certain sense, one can regard the three rock dwellers as morphologically and genetically (at least with mtDNA) cryptic species. Moreover, the colour pattern of *C. spongicola* seems less fixed than that of the other three species and usually resembles that of *C. woltereckae*, in few cases also *C. glaubrechtii*. This might hint at a less species-specific and still variable colour pattern in *C. spongicola*, but besides minor morphological differences, the choice of habitat of *C. spongicola* differs greatly from the rock dwellers. In 15 dissected sponges a high number of *C. spongicola* specimens were found (maximum 137 in a single

sponge), and only single specimens of two other species (*C. lingkonae* and *C. striata*) were found on the sponges as well (von Rintelen et al., 2007b; KvR personal field observation). The specimens from three populations of *C. glaubrechtii*, which group with morphologically very different species, show no apparent morphological differences to the remaining populations. Again, introgressive hybridization could play a role, but also the existence of cryptic species cannot be excluded as those populations form a coherent geographic cluster in Lake Towuti. The species boundaries of the three rock dwellers may not yet be as fixed as in most other Malili species, but this is probably just a question of time

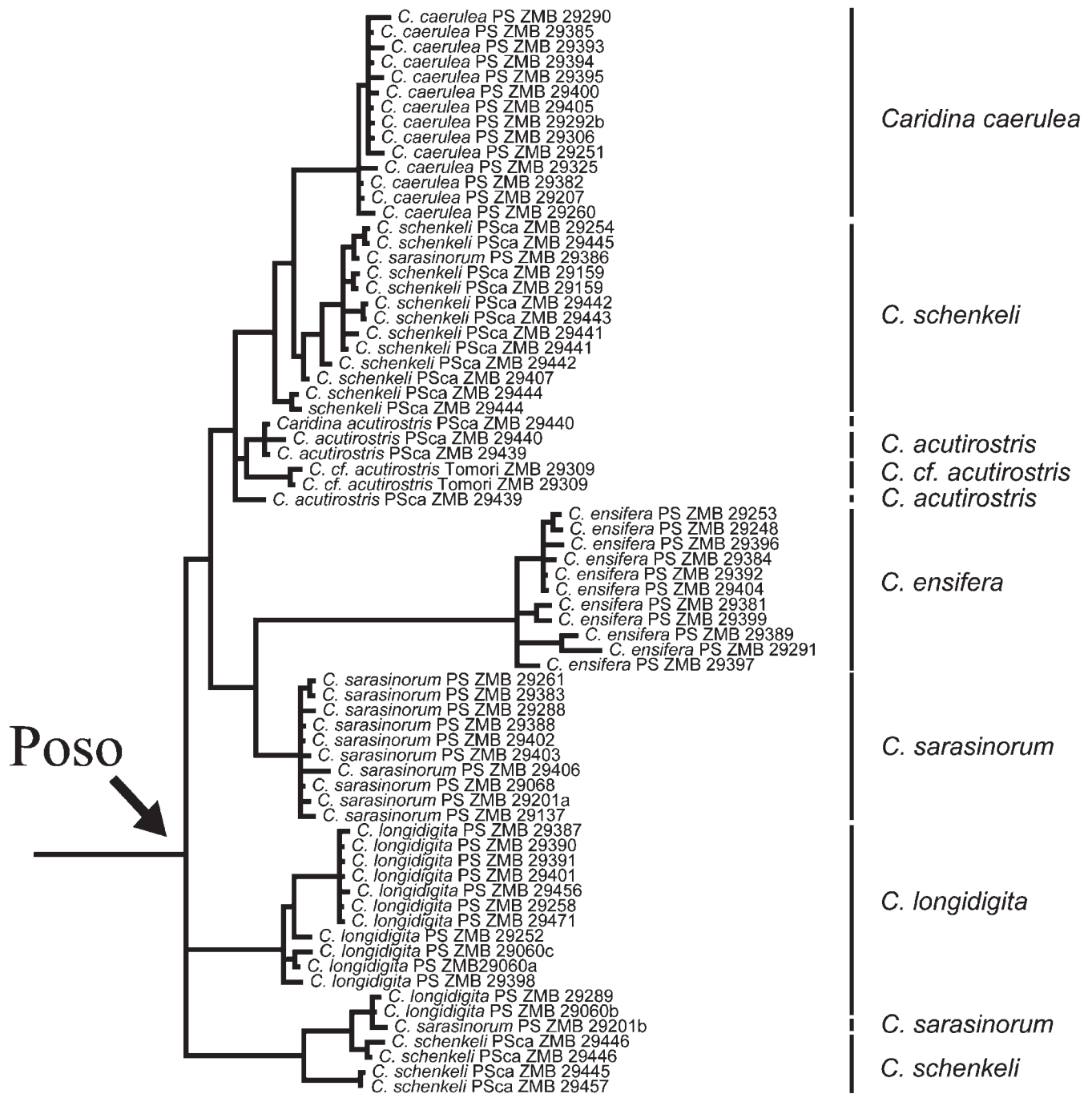


Fig. 65. Bayesian Inference phylogram (mtDNA, 16S and COI) showing taxa within the Poso clade (tree topology from von Rintelen et al., in review). For each sequenced specimen museum accession numbers are provided. Locality abbreviations (compare Fig. 1): PS (Lake Poso), PSca (Lake Poso catchment).

since the colour pattern obviously seems to be an effective delimitation factor in the other taxa (compare von Rintelen et al., 2007a, b, in review).

In cases involving allopatric populations of a single species, the problem of species delimitation of allopatric taxa arises, e.g. the Towuti versus Mahalona populations in *C. tenuirostris* or the Matano versus Mahalona/Towuti populations in *C. lanceolata* (Fig. 64), which form separate and genetically sufficiently distant clades. Roy et al. (2006) discussed the possibility that *C. lanceolata* might comprise cryptic species, because they found larger sequence divergence between allopatric populations from Lake Matano and Mahalona. Following their argument would mean to accept that *C. tenuirostris* also comprises two species, since distances between the two clades of that species are comparable to that of *C. lanceolata*. However, the approach taken here is not to split morphologically and ecologically indistinguishable (allopatric) populations into separate species, particularly if they are sister group to each other.

#### Conservation implications for the ancient lake species of Sulawesi

We found a higher number of species than previously described. This is by no means a rare phenomenon in endemic organisms from the ancient lakes of Sulawesi. The species diversity in other groups was likewise much higher than expected, e.g. in snails (von Rintelen et al., 2007c). Several authors discuss the possibility of the extinction of endemic species from Sulawesi and the ancient lakes (Whitten et al., 1987a, b; von Rintelen et al., 2007c, in review). They hint at the various threats in these lakes posed by introduced predator fish (e.g. tilapia, snakeheads, and carp), the Canadian nickel mine P.T. INCO at Lake Matano, the quantities of waste directed into the lakes from the rapidly expanding human population and the unlicensed export of native specimens. Further, illegal logging around the lakes' shoreline can cause erosion and subsequent landslides. Recently, not only the colourful species of *Caridina*, but also snails, crabs, and fishes from the lakes have caused a sensation in commercial aquarium trade and tens of thousands of specimens were exported to various countries, especially to Germany (Chris Lukhaup, pers. comm. 2007). In addition, in standard aquatic toxicity tests members of the shrimp genus *Caridina* from Java, Indonesia, showed a higher sensitivity for some chemicals than other freshwater crustaceans (Suchahyo et al., 2008) and the species of *Caridina* from the ancient lakes thus seem even more threatened by human impact.

The shrimps' diversity of colourful species is only one aspect of the fascinating fauna of Sulawesi's ancient lakes. They are also home to many rare and unusual species and communities, for example the first shrimp-sponge association described in freshwater organisms (von Rintelen et al., 2007b) or the numerous endemic and often colourful fishes, snails, and crabs that make the lakes similarly worth of protection as e.g. the Galapagos Islands. Some of the locally restricted species with partly very small populations, especially the

colourful ones, are highly endangered of becoming extinct. Thus, sampling of living specimens should be sensibly limited and other precautions are necessary to preserve the species diversity in the ancient lakes of Sulawesi also for future generations.

#### ACKNOWLEDGEMENTS

Thomas von Rintelen and Matthias Glaubrecht (ZMB) kindly helped collecting specimens and financed part of the fieldwork. We thank both for the great opportunity to work on the fauna of the fascinating lake systems of Sulawesi. Ristiyanti Marwoto and Daisy Wowor (MZB) greatly supported the fieldwork in Indonesia and gave overall logistic support. PT. INCO in Soroako, Indonesia, provided logistic support at the Malili lakes.

Carsten Lüter (ZMB) financially supported a field trip in 2004. The Advancement of Women (Frauenförderung, ZMB) supported the first author of this study with two travel grants and the purchase of a graphic software suite for preparing the figures. Chris Lukaup (Bittenfeld, Germany) provided most of the beautiful colour pictures presented in this study. Rainer Masche (Heidelberg, Germany) kindly provided the colour pictures of *Caridina tenuirostris* and *C. profundicola*. Many thanks to the following people for collecting some specimens: Arne Nolte (University Cologne, Germany), Peter Koller (University Regensburg, Germany), Fabian Herder and Joachim Frommen (Museum Koenig, Bonn, Germany), Rebecca Lamers and Andreas Wessel (ZMB). We further thank two anonymous referees for their valuable comments and their stamina while reading the long manuscript.

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